CHEMICAL COMPOSITION OF PLANTS AS AN INDEX OF THEIR NUTRITIONAL STATUS

by

D. W. GOODALL. Ph.D., D.I.C., F.L.S.

and

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Price 9/-

Published by the **Imperial Bureau of Horticulture and Plantation Crops**, East Malling, Kent, England and obtainable from I.A.B., Central Sales Branch, Penglais, Aberystwyth, Wales

July, 1947.

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FOREWORD

" Timeliness and promise " have been claimed as proper tests of the value of a projected scheme of scientific investigation. To completed work a third test, that of performance, must be added. In this Technical Communication from the Bureau of Horticulture and Plantation Crops there is to be found not only timeliness, but also a promise of further benefit to agriculture following on performance.

A judgment of the mineral needs of a crop is a problem perennial in agriculture, so a memoir of this kind cannot fail of timeliness. A critical study of the plant-analysis method as a means to determine the mineral needs of the plants—and hence in the language of technology their " nutritional status "—is all the more timely when, as at the present day, the " trace " elements seem as important in plant nutrition as vitamins in the food of animals.

It can be claimed also that this memoir stands just as high by the test of performance. The various techniques of plant analysis have been widely used by many workers, but all too often a technique has been accepted without critical consideration, and on the analytical data obtained there have been based claims as to fertiliser treatment which cannot be substantiated.

In this communication the authors estimate the value of these plant analysis methods with all the critical, methodological apparatus of modern biological research. They also indicate by what techniques and in what circumstances valid results may be obtained. Furthermore, the reader will find the results of previous workers assembled here with a thoroughness which will excite the gratitude of all working in this field.

How heavy the task of compilation must have been is brought home to one by mere inspection of the huge tables (e.g., II, III and XII) with their hundreds of analytical data, and also by the author-index of over 800 entries.

How valuable the plant analysis method should be in agricultural advisory work is here clearly brought out, provided always that sound field work, on the lines indicated, has determined for the various elements the " standard values " which point to sufficiency or deficiency. As against the method of field trials the chemical composition method is much less laborious, and has the great advantage of enabling one to obtain data of mineral requirements sufficiently early to allow of fertiliser treatment of the crop during the same growing season. How striking may be the close linkage between chemical composition and crop yield is shown by the work of F. Crowther on cotton in the Sudan Gezira, where the nitrogen content of the leaves two months after sowing enables one to forecast with fair accuracy the final yield of the crop.

In this memoir, then, a promise of future benefit to agriculture clearly follows on performance. All workers in the field of plant nutrition—plant physiologists as well as agriculturists—owe much to the authors, who are themselves exponents of the most modern branch of applied plant physiology, i.e., crop physiology.

The subject index is of remarkable fullness and renders easy of access the closely packed information of the memoir. In fairness to the authors it should be added that the manuscript was completed in 1945.

V. H. BLACKMAN.

February, 1947.

INTRODUCTION

METHODS FOR THE DIAGNOSIS OF THE FERTILIZER REQUIREMENTS OF PLANTS

FROM the time of Liebig, the establishment of whether, in any particular instance, the amounts of nutrient elements absorbed by the plant from the medium in which it is growing are adequate to its needs has been a most important preoccupation of plant physiologists and agricultural chemists.

FIELD TRIALS.

The most direct way of answering this question is, of course, to try the effect of additional amounts of nutrients, usually applied to the soil as artificial fertilizers, on the growth of the plants. Among the earliest of such experiments were the classical field trials at Rothamsted (Lawes and Gilbert, 1895), and these were followed by many others. It soon appeared, however, that generalizations could be drawn from the results of field experiments only with the greatest caution ; the effects of identical treatments on plant growth and yield varied greatly in different localities and seasons. In addition, field trials involved very considerable expenditure of time and money, and these considerations limited the utility of the method in practice. Nevertheless, in spite of the trouble and expense involved, and the uncertainty of generalizations drawn from them, field trials have during the past hundred years been set up on an ever-increasing scale ; there is no doubt that this will continue, whatever other methods for determining fertilizer requirements may be developed, for *at a particular situation and under given circumstances* the field trial represents the ultimate test to which the findings of any other proposed method must be submitted—if predictions founded on results of any other method fail to be confirmed by the results of field trials, such a method must be regarded as unsatisfactory.

POT CULTURE METHODS.

As soon as the difficulties attending field trials became evident, the possibility was envisaged of conducting trials on a much smaller scale in pot culture, where the growth conditions other than those immediately concerned could be controlled to an extent impossible in the field. Pot culture experiments of this type have been set up wherever plant nutrition has been studied, and, especially in the form proposed by Mitscherlich (1925), their use has been adopted at certain European centres as a routine method for determining the fertilizer requirements of soils. The work of Mitscherlich and his school (as well as his critics) has been reviewed in detail by Stewart (1932) and Behrens (1935). Among other pot culture methods for the determination of fertilizer requirements may be mentioned those of Greisenegger and Vorbuchner (1918), Wiessmann (1927), Fraps (1912, 1931), McDonald (1933a), Gilbert and Pember (1935), Capo (1938), and Ferres and Trumble (1943). But all pot culture methods for nutritional diagnosis suffer from the fact that the volume of soil accessible to the roots of the plant in the pot is generally very much less than in the field, and that the structure and composition of the soil in the pot are also different. Consequently, results obtained in pot cultures can only be applied to conditions in the field with considerable reserve—and in fact it has often been found that responses of plants in pot culture to a treatment do not tally with responses to the same treatment in the field (Gerlach, 1926 ; Neubauer *et al.*, 1928 ; Schuster and Stephenson, 1940). Further, nutrients are absorbed from the materials present in the soil to various extents by different species, which prevents the results of a pot experiment (or, for that matter, of field trials) being applied directly to other species growing in the same soil.

LEAF PAINTING AND INJECTION METHODS.

Another series of methods of nutritional diagnosis which may be regarded as bearing some relation to field and pot trials are those involving direct internal or external treatment with solutions of nutrients—by painting the leaves, or by the so-called solid and liquid injection techniques. These methods have been most widely applied in cases of chlorosis, where treatment with the deficient element causes the leaves to become green. In other instances the response may take the form of a local increase in size, or of a general increase in growth or yield. Painting methods have been mainly used for the diagnosis of iron deficiency (Gris, 1844 ; Gile, 1911 ; Parsche, 1936 ; Guest, 1943), but also for deficiencies of other trace elements (Bryan, 1929 ; Anderssen, 1932 ; Finch, 1933 ; Finch and Kinnison, 1933 ; Arnd and Hoffman, 1937 ; Chapman *et al.*, 1939 ; Chapman and Brown, 1941). Buslova (1939) and Roberts (1945a) have proposed a leaf-painting technique as a standard routine method. The diagnostic use of plant injection has been reviewed at length by Roach (1938, 1939 ; Roach and Roberts, 1945), who has put it forward as a routine diagnostic method.

The direct application of nutrients in this way has the advantage over soil application that no doubt arises that the materials reach the affected tissues ; in many cases also, results can be assessed in a much shorter time than after soil application. Their use, however, and in particular their interpretation, often demands considerable experience, and the results (especially of the smaller-scale methods) are very variable. In most cases where the methods have been successfully applied in practice, the deficiency has been sufficiently grave to cause marked symptoms ; whether they can be used to specify the fertilizer requirements of plants shewing only slight or no symptoms is still unproven.

SOIL ANALYSIS : CHEMICAL METHODS.

The difficulties early found to attend field experimentation led to attempts almost contemporaneously with the inception of the Rothamsted trials to circumvent this troublesome method (except occasionally for control purposes) by the very much simpler expedient of finding directly the amounts of nutrients present in any given field soil. But it was very early found that the different forms in which the nutrients occurred in the soil could be absorbed by a plant with different degrees of facility, and some forms could not be absorbed at all ; this led to the concept of " availability" of soil nutrients to the plant.

The nutrient elements in manures or fertilizers added to the soil were often found not to be immediately or completely ' available' to the plant– frequently only a small proportion of the added nutrients was actually taken up.

Over the next few decades, the main attention of those studying this problem was devoted to improving methods of soil analysis and testing different methods for extracting the "available" fraction of the nutrients. A number of trials were carried out with solutions of carbon dioxide, since this was thought to be the means by which roots were able to absorb insoluble constituents, but more satisfactory results were obtained with other weak acids. Some of these procedures, and others involving the determination of " exchangeable" bases adsorbed on the surface of colloidal soil particles were found to give results in very tolerable agreement with the results of field trials. These remarks, however, apply in the main only to determinations of phosphorus and potassium ; methods for determining "available" nitrogen supplies in the soil have never met with general acceptance on account of the importance of nitrification in the soil, and techniques proposed for determining the "available" soil supplies of the trace elements are as yet in a very early stage of development. A number of textbooks are available dealing *in extenso* with the many methods of determining chemically those fractions of soil nutrients thought to be of importance to plant development (Behrens, 1935 ; Wright, 1939 ; Piper, 1942a), so the subject need not be discussed further here.

The subject of chemical soil analysis should not, however, be left without mention of the recent attempts to develop rapid systems of soil tests, many of which can be performed in the field (Thornton *et al.*, 1934 ; Morgan, 1935, 1939 ; Hester *et al.*, 1937 ; Anderson and Noble, 1937 ; Spurway, 1938 ; Baver and Bruner, 1939 ; Merkle, 1939 ; Purvis and Blume, 1941).

SOIL ANALYSIS: BIOLOGICAL METHODS.

The progress made with chemical soil analysis over the past quarter of a century has not led agricultural chemists to become less aware that attempts to imitate the action of plant roots by chemical extractants can never hope to meet with full success—that working approximations are the most that can be expected. This has led many investigators to consider the possibility of using biological means of extraction.

Neubauer and Other Seedling Methods.

It was from this point of view that early investigators of plant analysis as a means of determining fertilizer requirements set out. Their ideas will be discussed in greater detail in the following section, but they never achieved widespread acceptance among their contemporaries, and it was not until the nineteen-twenties that biological methods of soil analysis came to be widely used. The first of these was one bearing the name of Neubauer—which has certain resemblances to that proposed much earlier by Wilfarth (1897); this method, originally described in 1923 (Neubauer, 1923; Neubauer and Schneider, 1923), has been discussed in detail by Stewart (1932) and Behrens (1935) and consists in growing rye seedlings on a limited quantity of the soil in question under controlled conditions for eighteen days. The soil is then considered to have been exhausted of nutrients; the seedlings are analysed for potassium and phosphorus, and the quantities found in excess of those in seedlings grown in pure sand, expressed in milligrams, are taken to represent the amounts of these nutrients available to the plant ("*wurzellöslich*") in the weight of soil used. Limiting figures for root-soluble nutrients are laid down for each crop species and the extent to which the amounts extracted fall below these limiting values indicates the need for fertilizer applications. The method attained very widespread acceptance in Germany and other European countries, but though it has been tested several times in the United States (Thornton, 1931, 1931a; Pettinger and Thornton, 1934; Stewart *et al.*, 1932) it has never been extensively used; the reason, doubtless, is that its potential advantages over chemical methods of soil analysis were not considered to outweigh the troublesome amount of manipulation entailed.

The question might be raised whether the Neubauer method, as a method involving the analysis of plant material, should not be discussed at length in the body of this communication, instead of thus cursorily in the introduction. However, as Stewart (1932) writes, "it is in reality very little different from any purely chemical method of determining availabilities"; in almost all the methods to be described in later sections, diagnosis is based on the *concentration* of the nutrients in the plant tissue, not on their total amounts; and in most the plants providing analytical material have not been grown specially for the purpose, but form part of a normal field crop.

Other workers have developed modifications of the Neubauer method using wheat seedlings (Ames and Gerdel, 1927) or even tree seedlings (for forest soils) instead of rye. Süchting's method (Süchting *et al.*, 1938; Süchting, 1939, 1942) with tree seedlings also deviates from Neubauer's technique in that the plants are grown for a whole season and—as also in the work of Ames and Gerdel—account is taken not only of the total amount of nutrients taken up, but also of their percentage in the plant dry matter.

By use of micro-organisms

Yet other biological methods of soil analysis have involved growing micro-organisms on the soil in question. A good account of work in this direction is given by Behrens (1935, 1937). Some of these methods display a certain affinity to that of Mitscherlich since it is on the growth rate of the test organisms that the conclusions are based, but they are all conveniently mentioned together here. The organisms used have included *Azotobacter* (Christensen, 1906, 1911, 1914, 1922; Niklas and Hirschberger, 1924; Truffaut and Bezssonoff, 1927; Winogradsky, 1928), *Bacterium globiforme* (Nicol, 1939); *Aspergillus niger* (Butkevič, 1909; Kosceleckiĭ, 1909; Benecke and Söding, 1927; Niklas *et al.*, 1930, 1930a; Simakova and Bovschik, 1932; Sekera and Schober, 1934; Mehlich *et al.*, 1935; Sartory *et al.*, 1935; Mulder, 1938; Acock, 1941); *Rhizopus* (Seidel, 1931); *Cunninghamella* (Mehlich *et al.*, 1934); and algae (Morgan, 1933).

Comparative tests (Dirks and Scheffer, 1928; Mehlich *et al.*, 1933; Scurti, 1940) have not generally shewn any marked superiority of the biological methods of soil analysis over the better chemical methods. There are, however, certain disadvantages common to all methods of soil analysis, whether biological or chemical, when used to determine fertilizer requirements. These rest on the fact that they cannot, as indicated above, reproduce the conditions under which the plant growing in the field absorbs nutrients from the soil. This applies with especial force when it is desired to assess the nutritional conditions in a soil to which localized applications of fertilizer have been made—by a combine drill, for instance, or by band placement. The difficulties in the use of soil analysis in relation to nitrogen and the trace elements have already been mentioned.

PLANT ANALYSIS METHODS

Reference has already been made to the analysis of plants growing in the field as a biological method of soil analysis. But plant analysis has relevance in a rather different respect to our central problem—the determination of fertilizer requirements. For if it can be shewn that the composition of a plant indicates its nutrient uptake or its nutrient needs—irrespective of the nutrient supplies in the soil—there becomes available a much more direct method than any technique for determining the "available" nutrients of the soil—which can be of interest only indirectly. It has in fact often been claimed that the composition of the plant does reflect its nutritional status—the adequacy of its nutrient supplies and the probability of its response to increased supplies. The examination of these claims will be the principal topic of later pages.

USE OF DEFICIENCY SYMPTOMS

The last group of methods of nutritional diagnosis which have been widely used are those based on abnormal development of the plant when nutrition is unsatisfactory. This abnormal development takes many forms of which the most common are chlorosis and necrosis of the leaves. It often happens, however, that the symptoms of a nutritional disorder are characteristic enough to be recognized with some certainty, and several atlases of plates (Hambidge, 1941; Chilean Nitrate Educ. Bur., 1941; Wallace, 1943, 1944) have been published shewing the symptoms produced by deficiency or excess of different elements in different species of crop plants. The recognition of a definite syndrome resulting from a particular nutritional disorder has been a principal contribution of the method of water culture to nutritional diagnosis. In general, the intention has been that such symptoms should be recognized as and when they occur in plants grown in the course of normal agricultural or horticultural practice. The suggestion has been made, however, that small plots of plants specially susceptible to particular deficiencies should be planted specifically for this purpose; such plants are described as indicators (Jones, 1929; Piper, 1940; Wallace, 1943, 1943a; Reeve *et al.*, 1944). As a means of assessing the boron status of soils, the growing of sunflowers in pots under controlled conditions has been suggested, the time needed for the appearance of symptoms being taken as an inverse measure of the boron supply in the soil (Colwell and Baker, 1939; Schuster and Stephenson, 1940; Colwell, 1943). Others have suggested the observation of symptoms on common weeds—those of potassium deficiency on charlock, for instance (M. N. Nicholson, private communication)—as an indication of the fertilizer requirements of crop plants.

Where a disorder can be diagnosed on the sole basis of symptoms occurring in the field, this is obviously a very quick and cheap method of ascertaining the plants' needs.

But the type of symptom induced by a nutrient deficiency varies from species to species, and sometimes even from variety to variety (Wallace, 1943; Hill and Johnston, 1940; Boynton *et al.*, 1941; Lineberry and Burkhart, 1944), and may be affected by the supply of other elements (Richards, 1944). Moreover, different disorders may give similar symptoms (Eaton, S. V., 1935; Nightingale, 1937; Boresch, 1938; Chapman *et al.*, 1939; Chapman and Brown, 1941, 1941a, 1942; Wallace, 1943; Boynton *et al.*, 1943; Bathurst, 1944; Drosdoff and Kenworthy, 1944), or the symptoms of a nutritional disorder may resemble those produced by some quite different cause (Haas, 1937; Spencer and Lavin, 1939; Shear and Ussery, 1940; Gardiner, 1940; Hoffer, in Hambidge, 1941; Burkhart, 1941; Wallace, 1943). Consequently the method

demands a high level of discrimination, and sometimes confirmation by other techniques. Another limitation to the value of symptoms as diagnostic indices lies in the fact that they usually indicate only the most severe deficiency—the effects of inadequate supply of other nutrients are masked (McMurtrey, in Hambidge, 1941). Further, it has fairly often been found that nutritional deficiencies may cause diminutions in yield without inducing any other symptoms (Mitchell, 1934; Arnd and Hoffmann, 1937; Berger and Truog, 1939, 1940; Roach, 1940; Batjer and Degman, 1940; Burkhart, 1941; Ulrich, 1943; Hill, 1943): this suggests that a more sensitive method than the observation of symptoms may often be required.

OTHER METHODS OF NUTRITIONAL DIAGNOSIS

Among other methods of deficiency diagnosis which have been tentatively investigated may be mentioned the work on absorption of nutrients from solutions by isolated discs of leaf tissue (Emp. Cott. Gr. Corp., 1942, 1943) and by seedlings transplanted from the soil under investigation (Lazurskii, 1939, 1940). These methods are attractive from the theoretical point of view, but would be difficult to apply on a large scale in practice.

Ecologists have from time to time suggested the botanical composition of the natural or weed flora as an index of the nutritional conditions prevailing in the soil on which it grows (Müller, 1915; Rademacher, 1935; Walsh, 1942; Gdnrs' Chron., 1942). In particular, the presence of calcifuge species such as *Scleranthus annuus* and *Rumex acetosella* has been proposed as an indication of the necessity of liming (Christensen and Larsen, 1910; Eichinger, 1929). While the general dependence of the distribution of species on nutrient supplies may be accepted, rarely is the effect clear enough to be practically useful; this principle seems, however, to have found some application in identifying those areas in the United States where the amounts of selenium in the soil were high enough to cause danger of toxic effects in mammals (Byers *et al.*, 1938; Beath *et al.*, 1939)—such areas seem to be characterized by the presence of certain species of *Xylorrhiza, Stanleya, Oonopsis* and *Astragalus*.

The fact that nitrogen deficiency is usually characterized by a pale yellowish-green colour has led some workers (Gassner and Goeze, 1936; Borden, 1942) to suggest chlorophyll determinations as a means of assessing nitrogen requirements; it is found, in fact, that a diminution in chlorophyll content can be shewn as a result of a degree of nitrogen deficiency not detectable by the appearance of the plant to the eye. Gassner and Goeze (1936) proposed a detailed technique for finding nitrogen requirements by chlorophyll determination which involved the growing of rye for 25-30 days in pots of soil and simultaneously in sand with different nitrogen supply levels. More recently, chlorophyll determinations have been recommended by Boynton and Compton (Boynton, 1945; Boynton and Compton, 1945; Compton and Boynton, 1945) for assessing the nitrogen status of apple trees.

This completes the introductory review of the different methods of assessing fertilizer requirements. A detailed consideration of the various methods which have been proposed making use of plant analysis will now be embarked upon, and later their value will be compared with that of the other techniques described above.

HISTORICAL

EARLY WORK ON DIAGNOSTIC PLANT ANALYSIS

Soon after the importance of the supply of nutrients from the soil for plant growth was recognized, and before the extent to which this supply varied in different soils was realized, the view was put forward, particularly by von Liebig (1840), that if soil fertility was to be maintained the quantities of nutrients removed from the soil in crops would need to be restored to it in the form of applications of manures or fertilizers (" Law of Restitution "). To apply this rule, it was necessary to know the average composition of the parts of crop plants harvested. But as knowledge on the varying response of different soils to different manurial materials accumulated, it became generally appreciated that, however true the " Law of Restitution " might ultimately be, it provided no guide whatever to the economic use of fertilizers.

The first investigator to have conceived the idea of using plant analysis as an index of available nutrient supplies appears to have been Weinhold (1862, 1864). He set out from the assumption that the plants growing naturally in any location in greatest abundance would be those whose nutrient needs the soil was best fitted to supply. Hence, these plants should contain nutrients in similar proportions to the assimilable nutrients of the soil, and the composition of the most abundant wild plants should provide information on the nutrient status of the soil. A corollary of this line of reasoning was that, when more than one species was abundant in a locality, all such species should be similar in nutrient composition. This was first tested (1862) on arable weeds, and found not to hold ; Weinhold considered that this might be due to the effects of cultivation on interspecific competition, and that plants growing on a virgin soil might agree better in composition. Later, however, (1864) he was able to test the hypothesis on the vegetation of a woodland soil ; though the agreement was better than for arable weeds, it was so far from satisfactory that Weinhold concluded that the physical properties of the soil were more important for plant competition than its chemical characteristics, and he abandoned this line of work.

Three years later, Hellriegel (1867) published the results of sand culture experiments with barley in which he found that the potassium content of both grain and straw increased with increasing potassium supply. He concluded : " In order to give a maximum yield, barley must be able to take up at least 5 parts of potash to every 1,000 parts of straw dry-matter and 3.8 to every 1,000 parts of grain dry-matter." The following year, at a conference of agricultural chemists, Hellriegel (1869) pointed out the disadvantages of chemical soil analysis, and suggested that analyses of harvested plant material might provide a better index of available nutrients in the soil; "if the necessary foundations are first laid by field trials, crop analysis will provide a satisfactory basis for the determination of both the relative and absolute proportions of plant nutrients present and available in the soil, and can suitably give the supplementary information needed to evaluate the results of soil analysis." Although his experimental work on the subject was slight, Hellriegel's ideas proved very stimulating to European investigators during the next three decades.

In 1868 also, as a result of an extensive series of water culture experiments with oats, Wolff was able to suggest 0.3% CaO as the minimum content of the whole aerial parts at maturity which corresponded to satisfactory growth. Subsequent work on the same lines (1876, 1877) enabled him to publish figures in respect of each of the six principal nutrients, not only the necessary minimal content ("*absolut nothwendige Minimum*") being quoted, but also values for good average development. These figures are reproduced in Table XIV.

The next work in this field which it is necessary to note is that of Heinrich (1882). He objected to the work of Hellriegel (1869) on the grounds that whole plants had been analysed—which might be a cause of error if the proportions between the organs varied. He analysed for

nitrogen various parts of oats plants receiving high and low nitrogen supplies, and concluded "that the *roots* are the most appropriate organ for comparative investigations involving the determination of nutritional conditions in the soil," since " the roots at maturity are the more depleted the poorer the soil is. The whole of the available nutrients have migrated to the aerial parts of the plant, there to be used for assimilation and for the formation of new organs." The choice of roots was supported because their composition was thought to be less liable than that of the aerial parts to influence by extraneous factors ; and Heinrich found the average root composition to be little affected by the loss of fine roots in the course of washing. He propounded a " Law of the Minimum " to the effect that when the supply of a nutrient was limiting growth its concentration in the root tissue declined to a certain minimal value. Minimal percentages were laid down for the content of the six principal nutrient elements in the dry matter of oat roots at maturity (see Table VII), and if in a sample under investigation the content of an element was at the minimal level, that element was deficient ; if none of the nutrients was at the minimal level but the content of one approached more nearly to the minimal level than that of the others, the probability of a response was often indicated.

Heinrich's ideas were followed up by Haessner (1887) and von Dikow (1891). Haessner analysed the roots of barley plants from a fertilizer trial, but found only slight differences in composition ; this is perhaps hardly surprising since the fertilizer effects studied were *residual* effect of treatments applied to sugar beet during the previous year. von Dikow also investigated the composition of roots of barley plants receiving different fertilizer treatments in the field ; the " roots " referred to included parts of the plant below the " first node." Since the four plots receiving only nitrogen and phosphorus gave roots differing considerably in potassium content, it was considered that the minimum content for the latter element had not been reached, and no limiting value was quoted. The minimum for phosphorus was given as 0.13% P_2O_5 since three of the four plots receiving only nitrogen and potassium approximated to this figure ; and on similar grounds the minimum for nitrogen was given as 0.63%. The data did not indicate any " luxury consumption," such as was found by Heinrich, and von Dikow suggested that the range of mineral content of plant tissue was limited both above and below, and that Heinrich's " Law of the Minimum" should be supplemented by a " Law of the Maximum " ; until this maximum mineral content was attained, fertilizer applications did not have their maximum effect on plant growth.

Heinrich's proposed method was also tested by Helmkampf (1892) and by Stahl-Schröder (1904). Helmkampf analysed the roots of oats and wheat subjected to different manurial treatments ; the nitrogen content in all plots was close to Heinrich's minimal range-in agreement with the marked response to nitrate fertilizer ; the potassium content was increased by potassium supply, while the phosphorus content remained fairly constant at 0.40-0.48% P_2O_5 irrespective of phosphate fertilizer treatment, which was taken as indicating that the maximal value suggested by von Dikow had been reached. Stahl-Schröder carried out similar experiments, and agreed that root composition reflected the soil supply of nutrients ; weather conditions in different years were found to affect root composition considerably, but the potential value of the method in more extreme cases, especially where different fields on the same farm could be compared, was not doubted.

Unlike von Dikow and Helmkampf, Stahl-Schröder found abundant evidence of "luxury consumption," and rejected von Dikow's proposal of a "Law of the Maximum." He considered that von Dikow's results might be ascribed to excessive leaching during the washing of the roots. Both Helmkampf and Stahl-Schröder considered that the difficulties of preparing and washing the roots rendered them an unsatisfactory part of the plant to sample ; Stahl-Schröder moreover found that the fine roots, many of which were lost during removal from the soil and washing, differed considerably in composition from the coarse roots. Since both these workers had obtained satisfactory results with other parts of the plant (see below) they decided on these grounds to reject root analysis.

Shortly after the publication of Heinrich's work on oat roots, Atterberg (1886, 1887, 1887a, 1887b, 1888, 1888a, 1889, 1901) began a lengthy series of experiments in Sweden, both in sand culture and in the field. The crop plant used was again oats, but the various aerial organs and not the roots were analysed. As a result of these investigations he came to the conclusion that

analysis of the grain provided a better index of the nitrogen and phosphorus supply conditions than that of the straw, but that grain analysis was of little use in relation to potassium nutrition, since the content of potassium in the grain was small and varied little in accordance with changes in external supply. Accordingly, for determining the potassium status, analysis of straw was recommended, or of the whole tops of plants harvested at the flowering stage; the latter material could also be used for nitrogen and phosphorus analyses; on the other hand, the analysis of whole plants *at maturity* was deprecated, since results would be greatly affected by the varying proportion of grain and straw. In the grain a value of 1.6 to 1.7 for the ratio $\frac{N}{P_2O_5}$ was optimal, and if this ratio exceeded 2.0 phosphorus deficiency might be suspected unless the phosphorus content was above 0.9% P_2O_5 (1888a). For whole plants sampled at flowering time the optimal ratio was $N : P_2O_5 :: 100 : 45$ (1889). As regards potassium, provided the sodium content was high, yield began to suffer when the potassium content of the straw fell below 1.0% K_2O, and at a level of 0.37-0.38% deficiency symptoms appeared; if the sodium content was low, potassium deficiency symptoms might appear with as much as 1.0% K_2O (1888a). Atterberg also (1889) paid some attention to the ratio of nitrogen to potash—determined in the grain and straw respectively; he considered that this ratio should not exceed unity (1889). Calcium deficiency symptoms (1901) appeared when the calcium content was in the range 0.10-0.18% CaO. The composition of the plants was found to be affected by water supply and by spacing.

Minimal and average figures were quoted for the content of the principal nutrients (see Table XII), but Atterberg did not accept the idea of a 'maximum' postulated by von Dikow (1891) in fact he obtained some evidence (1888) that supra-optimal phosphorus supplies might continue to increase the phosphorus content of the plant even while they decreased the yield. The use of the minimal and average values he describes (1901) in this fashion: "Which nutrient is present in minimum may be determined in the following way: one compares the percentage nutrient contents found by analysis with the corresponding mean and minimum values for oats. The nutrient whose content is most below this mean, or exceeds it least, and approaches the minimum most closely, is in minimum." While plant analysis was considered to give better information on the nutritional status of the plant than soil analysis, it was recognized that the results of the former could not lead directly to conclusions on nutrient supplies available in the soil. Atterberg anticipated (1889), but apparently did not carry out, the extension of these methods to other crops.

Helmkampf (1892) tested Atterberg's proposed technique on material from the same manurial trial as that mentioned above in connection with his critical examination of Heinrich's method. He came to conclusions substantially in agreement with those of Atterberg, but considered analysis of the whole aerial part of the plant sampled at flowering time was the most promising procedure. Helmkampf did not accept the concept of "luxury consumption," and in accordance with this view regarded an increase in the nutrient content with fertilizer supply as a more important index of the need for that fertilizer treatment than the absolute level of the nutrient content. Januszewski (1895), in conformity with the results of Atterberg and Helmkampf, found analysis of wheat grain a useful index of the nutritional status of the plants. Stahl-Schröder (1904), too, tested Atterberg's proposed method and found treatments to have the expected effect on the $\frac{N}{P_2O_5}$ ratio in the grain, though the values found were considerably lower than those of Atterberg. This difference was ascribed to climatic differences between Peterhof and Kalmar, where the experiments of Stahl-Schröder and Atterberg respectively were carried out, and for the Peterhof region a ratio of 100 : 35-40 was regarded as satisfactory. The same climatic factors affected the $\frac{N \text{ in grain}}{K_2O \text{ in straw}}$ ratio, and for this values of the order of 100:75 were considered satisfactory in Kurland. The examination only of ratios between nutrients was not, however, thought adequate; attention should also be paid to the absolute nutrient content values. Stahl-Schröder expressed the view that more attention should be paid to data from straw analyses, but it was in the more extreme cases that plant analysis was likely to be most useful, and conclusions that an element was in adequate supply were thought in general to carry

a greater degree of certainty than conclusions that it was deficient—since many irrelevant factors might interfere with the uptake of a nutrient and cause apparent deficiency. He reported the results of a survey of the nutritional status of crops in Kurland carried out by plant analysis, and gave some instances where the results proved to be of practical value. He claimed that the results obtained with oats would generally apply also to other crops. Stahl-Schröder objected to Helmkampf's suggestion that the whole aerial parts should be sampled at flowering time on the grounds that it would not be easy to gather samples from a number of different sites at just the same stage of development, and even slight variation in the stage at which sampling took place might well be reflected in a difference in composition.

Joulie (1889) gave an account of a case where poorly-cropping land had been brought into excellent heart by combining the diagnostic use of plant and soil analysis. The original fertilizer régime was decided on a basis of the results of soil analysis; the crops grown subsequently were analysed, the values were compared with "*compositions types*" (averages of numerous data from plants of good growth), and nutritional deficiencies thus made apparent were remedied.

von Seelhorst (Liebscher *et al.*, 1898) reported an experiment in which oats were grown in pot culture on twenty-four soils, each receiving eight different fertilizer treatments. The plants were harvested just before the milk-ripe stage; their dry weights were determined and the material was analysed for nitrogen, phosphorus and potassium. The plant composition was found to be reasonably closely correlated with the fertilizer responses shewn in dry matter yield. Nutrient percentages in the plant material indicating that adequate supplies were available were deduced (Table XIJ), but it was emphasized that fertilizer responses could not be predicted from the percentage of one nutrient alone; for instance, a value for nitrogen content indicating the probability of a definite response to applications of a nitrogen-containing fertilizer, when supplies of other nutrients were fully adequate, would be associated with no such response if either potassium or phosphorus was in short supply. von Seelhorst concluded that under controlled growth conditions plant analysis could be used to determine fertilizer requirements and was more reliable than soil analysis; he pointed out, however, that conditions in pot culture were very different from those in the field. However, as part of the same scheme of work, an extensive series of field trials was also reported (Edler, 1898), many of which appear to have been at the same sites from which soil was collected for the pot culture experiments; though Von Seelhorst did not comment on this aspect of the work, there appears to be a moderate degree of correlation between the responses observed in the field trials—both with oats and potatoes—and the composition of the oat plants from the untreated pots.

Godlewski (1901) criticised the experiments reported by von Seelhorst on the grounds that the plants were grown in pot culture, and reported results from some field fertilizer trials carried out on wheat, barley and potato. From the wheat experiment samples were taken at flowering time, while for the other two crops the final harvested material was analysed—grain and straw, or tubers. From the potato tuber analysis, it was concluded that nitrogen was deficient if the the ratio $\frac{N}{P_2O_5}$ was less than 2, or $\frac{N}{K_2O}$ less than 0.6; when the potassium nutrition was inadequate, the ratio $\frac{K_2O}{P_2O_5}$ was less than 2.5 Similar limiting values (Table XV) were also quoted for the nutrient ratios in barley straw, which Godlewski regarded as more suitable than the grain: "This relationship is particularly evident in the composition of the straw; it is much less clear in that of the grain" In barley the ratio of nitrogen to the metallic nutrients was not thought to be of any importance. Hanamann (1904) also performed some analyses on barley plants subjected to various fertilizer treatments in pot culture and in the field. Root and grain analyses were not considered promising but the composition of the mature straw and of the whole tops sampled after flowering provided useful indications of fertilizer requirements.

Influenced by the original work of Hellriegel, Nanninga (1903, 1904) at Buitenzorg was led to study quite a different crop—tea. From a study of the composition of the ash of the tea leaf, he concluded that in general ash analysis would shew which elements were in inadequate supply in a poorly-cropping plantation. Since, however, he found no connection between the potassium content of the ash in the samples he studied and that of the soil, he concluded that in the

tea gardens of Java potassium was never in minimum. Leaf analysis was considered both quicker and more trustworthy than soil analysis as an index of mineral deficiencies. Remy (1903, 1903a, 1903b) considered the possibility of using leaf analysis to indicate the fertilizer needs of hops. From a few analytical results in fertilizer trials, he concluded that in respect of nitrogen and phosphorus, though not potassium, " the chemical composition of senescent leaves gathered at a particular level gives information on the fertilizer status of the soil". He chose the senescent leaves on *a priori* grounds, since under deficiency conditions they were depleted of nutrients to meet the needs of the regions of active growth. Limiting values (see Table VIII) for phosphorus content of these leaves were suggested (1903b). Schneider (1905) later confirmed that the differences in composition of the oldest leaves with different treatment were in fact more marked than in other parts in June, though later in the season rather younger leaves were to be preferred. Later, Remy turned his attention to other plants, and (1906) shewed that the same principle applied to oats—that differences in phosphorus nutrition were more evident in the composition of the older leaves and stems than in the growing regions. In apple trees (1906a), the leaves were again suitable organs to analyse for the purpose of indicating nutritional requirements.

Up to this time, all the work on this subject except that of Nanninga had been performed in continental Europe; but in 1905 Hall, then Director of Rothamsted Experimental Station, intervened in the discussion. He drew data mainly from analysis of harvested products from the long-standing field manurial trials at Rothamsted—grain and straw of wheat and barley, tubers of potatoes and roots of mangels. He found that differences in the composition of the plant ash with treatment were less marked than those in available nutrients in the soil; also the composition of the plant ash was subject to considerable seasonal variations. Of the materials mentioned, the only ones considered promising were barley straw, the ash of which shewed marked variations in potassium and phosphorus content with treatment, and—for potassium determinations—mangel roots. In another experiment, oats were grown in pot culture in six soils whose responses in the field to fertilizers were known; the plants were harvested before maturity, and the potassium and phosphorus content of their ash was found to be lowest on the soils responding to the respective fertilizers; but replicate pots shewed considerable variation in ash composition. Hall made some further observations on a series of eight fertilizer trials with swedes in different parts of England, and found the composition of the ash of roots from the untreated plots to be closely related to the observed response to fertilizer treatment. Even here, however, he did not consider that plant analysis would prove more useful than soil analysis. He concluded by expressing the view that to use analysis of crop plants as a method for determining fertilizer needs it would be necessary to set up special unmanured plots growing the plant in question; therefore, " some test plant must be found which grows pretty universally on all soils, in fact some weed of arable land that would always be available. . . . It is in the direction of finding such a test plant that I am now continuing the work." It does not appear, however, that Hall ever published any reports of his experiments on weed analysis, and—apart from a hint by Haddock (1934) in regard to *Chenopodium album* and magnesium deficiency and some negative results in Australia (Teakle, Thomas and Turton, 1941) on the possibility of using capeweed to indicate copper deficiency—this possibility seems to have remained uninvestigated until the work of Goodall (1945c) shewing that the potassium content of *Polygonum convolvolus* leaves may indicate the potassium requirements of barley.

Hall's paper appears to have had a discouraging effect, for the volume of work published on plant analysis as a diagnostic procedure declined markedly during the next two decades. Probably the development of improved methods of soil analysis was also in part responsible for this decline. But work on plant analysis for determining fertilizer requirements continued at Darmstadt and Breslau, and in Switzerland, and Jakuškin (1915) in Russia published an isolated investigation on phosphorus deficiency in cereals.

In 1907 Wagner and his collaborators described a series of fertilizer experiments with grape vines; in a set of long-term pot cultures, under different manurial treatments, the leaves and wood, and the juice and pulp of the fruit were analysed for nitrogen, phosphorus and potassium. It was found that analysis of the leaves shewed fertilizer differences better than that of the other parts. In healthy plants, it was stated, the leaves contained some 1.56% nitrogen, 1.24%

K_2O and 0.43% P_2O_5; vines with mineral content above this level would shew no response to fertilizer treatment. Later work (Wagner, 1911, 1924) led only to very small modifications in these figures. It was pointed out that the fruiting condition of the vine would affect the composition of the leaves—especially their potassium content—and that none of the three nutrients could be considered in isolation.

In 1875, Emmerling had mentioned a case where soil analysis had been supplemented by analysis of hay for the purpose of diagnosing the cause of unsatisfactory growth in a meadow, and making fertilizer recommendations; this work does not appear to have been continued, but in 1909 Wagner reported the results of fifteen field experiments on the manuring of meadows, extending over several years; he found that the potassium and phosphorus content of the hay varied greatly with the treatment, and was able to propose values for its percentage composition characteristic of different levels of adequacy of nutrient supply (Table IX). Subsequent work (Wagner, 1921) did not necessitate any alteration in these characteristic values. He considered the comparison of hay analyses with these characteristic values to be a very useful substitute for field fertilizer trials where the latter were impracticable. Wagner's proposals had to meet a certain amount of criticism (Remy, 1911; Stutzer, 1914; Haselhoff, 1918), but aroused considerable interest. Tacke (1910, 1910a, 1910b) found that Wagner's characteristic values applied satisfactorily to hay from German bogs and marshes, but von Feilitzen (1910, 1910a) considered that they were too high for conditions in Sweden. Müller (1915) in Switzerland tested Wagner's conclusions on samples from a series of nine fertilizer trials in different parts of the country and concluded that this method might even be more trustworthy than field trials. Liechti and Ritter (1917) also carried out an investigation on similar lines, as a result of which they proposed modifications in Wagner's characteristic values to meet Swiss conditions. Like Müller, they considered that the exact stage of development reached at the time of harvest would affect the composition of the hay; they also suggested that its chemical composition would to some extent depend upon the proportion of different species present. Mayr and Ahr (1919), in a careful critical study of the method, while regarding Wagner's general conclusions as confirmed by their work, considered that the botanical as well as the chemical composition of the hay should be taken into account. This point was the subject of several other criticisms of the method in later years (Raum, 1926; Kauter, 1935; Truninger and von Grünigen, 1935). Alway *et al.* (1926), in a series of fertilizer trials on ten clover-timothy fields, were unable to shew any relationship between the phosphorus content of the hay and the response to phosphate fertilizers. Nevertheless, hay analysis continued to be used extensively in Switzerland as a basis for fertilizer recommendations for grassland, with very satisfactory practical results (Wiegner, 1933). It has also been used in Holland (van Itallie, 1935; Hart and van der Paauw, 1942).

Wagner (1915) also reported the results of a very extensive series of rotational fertilizer experiments with field crops, and on this basis proposed the analysis of cereal straw, roots of beets, or tubers of potatoes as a means of characterizing the fertilizer requirements of arable soils. The limiting values he mentioned are cited in Table XII. Hoffman (1917) tested this possibility in regard to the potassium content of cereal straw, and concluded that the value of such a diagnostic technique was much less well established than in regard to hay analysis.

In the second decade of this century, Pfeiffer and his collaborators at Breslau returned to the attack on the problem of the diagnosis of the nutrient needs of cereals. At first their interest in the problem was casual; in the course of a paper on the effect of water, light and nitrogen supply on the growth and composition of oat grain and straw (Pfeiffer *et al.*, 1912), it was pointed out that the results had a bearing on the choice of an organ for analysis where the determination of fertilizer requirements was in question. "In the determination of limiting values at which nitrogen fertilizer applications begin to be unremunerative, the straw should perhaps be taken primarily into account." The attempts made by several workers (Wolff, 1876, 1877; Heinrich, 1882; Atterberg, 1901) to specify minimal percentages, an approach to which indicated deficiency, was criticised; to the Breslau workers it seemed that, on the contrary, "Maximal values at which further nutrient supply causes no increase in yield, at which luxury consumption in the true sense commences, must be determined, so that in any particular case it can be found how far the observed values fall below the maximum."

Subsequently (Pfeiffer *et al.*, 1915) an experiment was set up deliberately to test the possibilities of plant analysis for estimating soil nutrient supplies. The experiment was carried out in pots, since it was thought that control of water supply was important; oats was the test plant, and seven different soils were used. To some pots incomplete fertilizers lacking one of the three principal nutrients were applied, while others were left untreated. The plants were harvested at the milk-ripe stage and they were analysed for nitrogen, phosphorus and potassium. The point of view adopted was that the percentage of an element in the material from pots receiving fertilizer without this element would represent a minimal value ("*Normalgehaltszahl*"); and the extent to which the corresponding percentage in the control pot exceeded this minimal value would indicate the available supply of the nutrient in the soil in question. Though it was found in fact that the "minimal values" for nitrogen and phosphorus fell within a fairly narrow range, those for potassium varied greatly; evidently some of the soils were so well supplied with potassium that even under conditions of maximum yield luxury consumption was taking place. Since the uptake of potassium and phosphorus was increased by the application of fertilizers not containing these elements, it was not considered that analysis of plants from the control pots would give useful information on the availability of these elements. The relationships found with nitrogen were more satisfactory, and the mean "minimal value" found (0.759%) agreed passably well with that found by Liebscher *et al.* (1898) (0.649%). The suggestion was repeated that, in addition to the "minimal values" it might be desirable to establish "maximal values" for mineral content above which no yield increases should be expected.

Later, the Breslau workers (Pfeiffer *et al.*, 1919) performed a series of experiments in sand culture in which oat plants were supplied with eleven different levels of the three principal nutrients under different conditions of watering and illumination. The plants were harvested at the milk-ripe stage and analysed for the elements whose supply had been varied. Yield curves of the Mitscherlich type were deduced without assuming the constancy of the effect factor. The relation of the yield to the nutrient content of the dry matter was then studied. For one of the nitrogen series, a hyperbolic function was found to fit these data fairly closely. Since, however, it was desirable to find a way of eliminating the effect of the different shading and watering conditions, the assumption was made that "for those points on the yield curve where the gradient divided by the yield gives the same values, the yields in question correspond to the same percentage nutrient content." On this basis curves were drawn by trial and error, and were found to represent tolerably well the relationship between yield on the one hand and content of nitrogen and phosphorus on the other. The curves for potassium agreed poorly with the observed points. It was suggested that, from the yield and nutrient content of plants grown on a given soil, it would be possible to deduce the Mitscherlich curve on which they lay, and hence to deduce the probable response to any proposed fertilizer application. It was pointed out, however, that the nutrient content of plants grown in soil is generally higher with a given yield than in sand cultures; the yield responses to fertilizer treatment in the field would also differ from those in sand culture. Hence it would be premature to attempt to apply the results of these experiments to conditions in the field. Shortly after the publication of this paper, Mitscherlich (1919) tested the assumption that a given nutrient content of the plant material always corresponded to the same slope of the yield curve, but found it did not apply to the data he used, which involved a comparison of three phosphatic fertilizer materials. Lange (1926), too, came to the conclusion that his results with oats grown in pot culture on different soils did not bear out Pfeiffer's hypothesis.

Münter (1919, 1920) used data from a long-term rotational manurial trial to test the possibilities of plant analysis as a means of assessing fertilizer requirements. The material used was drawn from five consecutive years and eight manurial treatments, and the crops for which data were given were wheat and sugar beet. The only materials in which Münter considered that the percentage nutrient content could give a direct indication of the fertilizer requirements of the soil were the tops and roots of sugar beet, which could shew the phosphorus status (see limiting values, Table XII). For the other nutrients and for the wheat grain and straw the effects on composition of varying weather in the different years were held to be too great to make the use of these data possible.

For the nitrogen status Münter thought that the total uptake per unit area of ground pro-

vided a better index, and suggestions were also made of limiting values for certain ratios of the nutrients in the plant material (Table XV). He considered that the fertilizer requirements of a field could be best diagnosed by analysis of material from small plots treated, on the one hand, with nitrogenous fertilizer only, and on the other with a fertilizer containing potassium and phosphorus but no nitrogen.

The work described in the preceding pages has been discussed in some detail, not necessarily because it is intrinsically important, but because it has been almost forgotten. In reading much of the recent literature on the subject one receives the impression that the diagnostic use of plant analysis began in the nineteen-twenties, and reference is hardly ever made to the earlier work. However, although some of this earlier work rested on a rather inadequate experimental foundation and none of the investigators could make use of modern techniques of statistical analysis, some of the experiments they described will stand comparison with most recent work on the subject, and present-day experimenters can certainly learn from a perusal of their papers.

That work prior to 1920 has largely been forgotten is doubtless partly due to the great expansion since that date; but it must also be remembered that most of the earlier work was performed in German-speaking countries, and that in later years the interests of agricultural chemists in those countries have been concentrated upon the development of biological methods of soil analysis—particularly those of Mitscherlich and Neubauer. The great majority of investigations during more recent years on the diagnostic use of plant analysis have been carried out in English-speaking countries; the language barrier has probably increased the neglect of earlier work published in German.

RECENT WORK ON DIAGNOSTIC PLANT ANALYSIS

The reasons for the great expansion during the past twenty-five years in work on plant analysis for diagnostic purposes, which is in part the cause of the oblivion into which earlier work has fallen, are diverse. One is unquestionably the increasingly recognized importance of deficiencies of the trace elements. Another appears to be the increasing attention paid by agricultural chemists and agricultural research workers in general to the horticultural crops—in which deficiencies can not only more often be recognized during growth than in the field crops, but also more easily be remedied. A third contributory reason is doubtless the improvements which have been introduced into analytical technique—particularly those which have facilitated the rapid analysis of large numbers of samples, such as the development of colorimetric and spectrographic methods. Finally, the virtual abandonment by most investigators of the conception of plant analysis as a biological method of soil analysis, and its replacement by an interest in the nutritional condition of the plant itself irrespective of its relation to nutrient supplies in the soil played a part in the later development of these methods; as has already been shewn, many of the earlier workers were interested primarily in soil conditions, though von Dikow (1891) and Atterberg (1901) realized that plant analyses could be expected to give information mainly on the nutrient needs of the plants, and not of the soils.

Developments during the past quarter of a century in the diagnostic use of plant analysis can be discussed in the present section only in fairly general terms. Most of the investigations can be included in one of the groups below:—

(1) Investigation of nutritional disorders made manifest by definite symptoms.
(2) Interpretation of the results of field trials.
(3) Development of rapid testing methods for use in advisory work.
(4) Use of plant analysis as a method of nutritional survey.

These categories are, of course, far from mutually exclusive, but they will serve as convenient pegs on which to hang the following paragraphs.

Identification of Symptoms of Nutritional Disorders

We will first consider those investigations in which plant analysis has contributed to the recognition of symptoms of nutritional disorders. Such investigations have been carried out

at a great many institutions in all parts of the world, and the general course of events has been: (a) the disorder is distinguished from others and a clinical picture of the symptoms obtained; (b) attempts are made to identify its cause by soil analysis, analysis of affected plants, or tentative treatment with elements which it is thought may be deficient, or by trying to reproduce the symptoms in sand or solution culture; generally a combination of several of these methods has been used, and often the presence locally of deficiency diseases of other crop plants has provided important clues; (c) when these attempts have met with success, and (in most cases) have led to a satisfactory means of control, the symptoms alone can generally be used as a method of identification in particular cases, and only where the symptoms are doubtful, or (often) where the disorder is observed for the first time in a new region, is it necessary to confirm the diagnosis by some other technique—a role which plant analysis can often play.

In some instances the order of the first two stages has been reversed—symptoms of a disorder have first been induced in sand or solution culture, and have later been recognized in the field; but in such cases confirmation of the identification of the field symptoms is usually necessary.

Among the many nutritional disorders in which analysis of the affected plants provided the first clue to their etiology may be mentioned potassium deficiency of plum (Wallace, 1928b), grape-vine (Herschler, 1933), rhubarb (Carolus, 1936, 1938; Carolus *et al.*, 1938), tung (Drosdoff and Painter, 1942; Drosdoff, 1943), and peach (Dunbar and Anthony, 1943); calcium deficiency of the potato (Roach, 1945); magnesium deficiency of orange (Parbery, 1935), grapefruit (Fudge, 1938, 1939), pine (Becker, 1940), pineapple (Quiñones, 1940), tomato (Cromwell and Hunter, 1942) and tung (Drosdoff and Kenworthy, 1944); boron deficiency in orange (Morris, 1937); manganese deficiency in bracken (Hunter, 1942) and cherry (Duggan, 1943; Roach, 1944); copper deficiency in plum (Anderssen, 1932), grape-vine (Teakle *et al.*, 1943) and tung (Drosdoff and Dickey, 1943); chlorine toxicity in avocado (Haas, 1929, 1936); manganese toxicity in French bean (Parbery, 1941, 1943); and combined potassium, manganese and iron deficiency in deciduous fruit trees (Roberts, 1945). Instances in which analysis of plant material has provided confirmation of a tentative diagnosis based on other grounds are, of course, even more numerous.

Occasionally plant analysis has been used to correct an unjustified identification of symptoms. For instance, " frenching " of tobacco had been considered identical with the symptoms induced by thallium toxicity until it was shewn that no thallium could be found in " frenched " plants by spectrographic analysis, although it could readily be demonstrated in plants with even slight toxicity symptoms (Spencer and Lavin, 1939; Shear and Ussery, 1940). A chlorosis of peanut plants was thought to be nutritional until their composition was found to be normal, when it was identified as due to leaf-hopper injury (Burkhart, 1941). Analysis of the plant material has enabled spray injury to be distinguished from potassium deficiency in the apple (Gardiner, 1940) and cases of corky split veins due to boron deficiency and to other causes to be distinguished in citrus (Haas, 1945).

In view of the value of plant analysis in providing confirmation of an uncertain diagnosis by deficiency symptoms, a table has been prepared (Table I) in which many of the published data on the content of nutrients in plants shewing symptoms of nutritional disorders have been reproduced in summary form and contrasted with data for otherwise comparable plants not shewing the symptoms. The investigations from which these data are derived vary greatly in value; it is hardly possible to indicate this in the table—even the number of samples included has been omitted—but the information in column 5 shews one respect in which data from different sources are not fully comparable, giving the size of the unit from which each sample was taken and to which the statement as to the presence or absence of symptoms applies. If one assumes a limiting value for the content of a nutrient above which no symptoms appear, but that the content continues to increase above this level with increasing supply, it is clear that a sample for analysis taken at random on a plot where only some plants shew symptoms will not represent those plants properly, and may even shew a higher content of the deficient nutrient than a sample from another plot without symptoms. It has not been possible in the table to distinguish between different intensities of symptoms, so (except in cases indicated by the footnote (Q)) the figures in columns 7 and 9 represent the extreme range for all samples drawn from material shewing

symptoms, no matter how slight, while those in column 8 give the extreme range for samples from areas, plants or organs showing no symptoms whatever. Varietal differences have not in general been indicated, and the ranges of composition shewn often include data from several varieties; most investigators agree, however, that varietal differences in nutrient content are usually relatively small (see pp. 113-114).

The symptoms included in Table I are all recognizable abnormalities, and not merely delays or reduction in flowering, reduced or spindly growth, or paler leaf colour.

It will be noted that Tables I and II contain no reference to iron deficiency. The reason for this is that the relation between iron deficiency and the iron content of the plant is still very far from clear. Many chloroses can be cured by a superficial application of a solution of ferrous sulphate to the leaves in the form of a paint or spray, or by injection of iron compounds; and yet the chlorotic plants are often found to contain no less—or even more—iron than normal ones (Gile, 1911; Averna-Saccá, 1912; Milad, 1925, 1939; Oserkowsky, 1932, 1933; Wann, 1934; Olsen, 1935; Iljin, 1943; Lindner and Harley, 1944; Roach, 1944). Admittedly, a number of other cases have been reported where the iron content of the chlorotic leaves is subnormal (Wallace and Mann, 1926; Wallace, 1928; Loehwing, 1928; Ravaz *et al.*, 1928; Chapman, 1931; Scholz, 1933; Milad, 1939; Guest, 1943; Thorne and Wallace, 1944; Bennett, 1945); but the relationship does not appear to be at all regular or trustworthy, though occasionally (Guest, 1941) analysis has given useful diagnostic indications. According to Jacobson (1945), surface contamination may be responsible for much of the disagreement between iron deficiency symptoms and iron content of leaves. The suggestion has been made (Oserkowsky, 1933) that only a certain fraction of the iron present in the plant is "active"; Oserkowsky himself identified this "active" iron with that soluble in N hydrochloric acid, but Lindner and Harley (1944) found that in lime-induced chlorosis the fraction soluble in 0.5 N hydrochloric acid but not in 0.1 N hydrochloric acid was most consistently related to the symptoms, though this did not apply to other types of chlorosis curable by iron. It appears that for the present reliance must be placed on methods other than plant analysis for the diagnosis of iron deficiency.

Table I.

Content of nutrients in plant material in relation to the incidence of deficiency or toxicity symptoms.

N.B.—Letters in columns 3—5 and 7—9 refer to Notes at end of Table.

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated. Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
APPLE (*Pyrus malus*, etc.)									
	K	A	————	J	Leaves	0.23-0.35	0.41-1.61 (Q)		Wallace 1931
	K	D	Oct.	J	Leaves	0.33-0.68	0.83-2.31		Batjer & Degman 1940
	K	A	July-Aug.	J	Leaves	0.28-0.90	0.56-1.49		Reuther & Boynton 1940
	K	A	Sept.	J	Leaves	0.25-0.46	0.49-0.66		Burrell & Cain 1941
	K	D (?)	————	I	Leaves	0.37-0.59	1.70-2.90		Edgerton 1941
	K	A, B_I	July-Aug.	J	Leaves from middle of terminal shoots	0.28-0.95	0.40-1.56 (Q)		Reuther 1941a
	K	B_I	Late July	I	Shoot leaves	0.56-0.58	1.16-2.18		Burrell & Boynton 1943
	K	B_1, D	June-Sept.	I, K	Leaves	0.6-0.75	1.01-3.0		Boynton & Burrell 1944a
	K	A	July-Oct.	J	Leaves	0.45-0.93	1.53-2.04		Goodall 1945
	K	B_I	July-Sept.	I	Leaves	0.57-1.01	0.73-1.86		Nicholas & Jones 1945
	K	D	Nov.	J	Bark	0.639-0.740	0.682-1.049		Batjer & Degman 1940
	Mg	D	June-July	J	Leaves	0.0628-0.0937	0.1179-0.4140		Wallace 1929
	Mg	A	Feb.-Mar. (F)	G	Leader tip leaves	0.17-0.38	0.32-0.78		Kidson *et al.* 1940
	Mg	A	Feb.-Mar. (F)	G	Older leader leaves	0.052-0.17	0.22-0.45		Kidson *et al.* 1940
	Mg	A	————	G	Leaves	0.72-1.51 (N)	3.0-4.2 (N)		Hill & Johnston 1940
	Mg	A, B_I	July-Sept.	G, I	Leaves near base of terminal shoots	0.05-0.19	0.18-0.29		Wallace 1940
	Mg	B_I	July	I	Older leaves of current season's shoots	0.13-0.18	0.14-0.19		Wallace 1940a
	Mg	A, B_I	————	—	Leaves	1.3-3.3 (N)	3.0-4.9 (N)		Hill 1941
	Mg	B_2	July	L	Median shoot leaves	0.02-0.33	0.21-0.53		Boynton *et al.* 1943
	Mg	B_I	Midsummer	I	Median shoot leaves	0.07-0.19	0.11-0.21 (Q)		Boynton *et al.* 1943
	Mg	C	July	I	Leaves	0.23-0.47	0.64-1.13		Southwick 1943
	Mg	A	Aug.	J	Median shoot leaves	0.09-0.23	0.23-0.35		Southwick 1943
	Mg	B_I, D	June-Sept.	I, K	Leaves	0.08-0.20	0.16-0.72		Boynton & Burrell 1944a
	Mg	A	July-Oct.	J	Leaves	0.138-0.184	0.191-0.289		Goodall 1945
	Mg	B_I	July-Sept.	I	Leaves	0.05-0.23	0.20-0.25		Nicholas & Jones 1945
	Mg	B_I	July	I	Median shoot leaves	0.08-0.20	0.11-0.27		Boynton 1945a
	Mg	A, B_I	Early summer	I	Petioles (2% acetic acid extract)	0.0125-0.0250 (O)	0.0500-0.0750 (O)		Hill & Johnston 1940

Mg	D	Dec.-Jan.	J	Shoot bark	0.088	0.163-0.293	Wallace 1929
Mg	D	Dec.-Jan.	J	Shoot wood	0.042	0.0743-0.0834	Wallace 1929
Mg	D	Dec.	J	Trunk bark	0.0651-0.0669	0.1620-0.1860	Wallace 1929
Mg	D	Dec.	J	Trunk wood	0.0136-0.0168	0.0316-0.0446	Wallace 1929
Mg	D	June-July	J	Stems and petioles	0.118-0.159	0.192-0.330	Wallace 1929
Mg	A, B_1	Early summer	I	Terminal shoots (2% acetic acid extract)	0.0750 (O)	0.1000-0.1500 (O)	Hill & Johnston 1940
B	A	————	K	Leaves	0.0009-0.0011	0.0017-0.0018	Askew, 1935
B	A, B_2	————	K	Leaves	0.00151-0.00204	0.00250-0.00346	Askew & Chittenden 1936
B	B_1	Feb. (F)	I	Leaves	0.00126-0.00257	0.00213-0.00281 (Q)	Askew *et al.* 1936
B	A	————	K	Leaves	0.000481-0.000683	0.001080-0.001826	McLarty *et al.* 1936
B	B_1	————	K	Leaves	0.00102-0.00150	0.00133-0.00280	Woodbridge 1937
B	A	————	G	Leaves	0.00048-0.00161	0.00108-0.00247	Woodbridge 1937
B	A	————	K	Twigs	0.000649-0.000930	0.001135-0.001417	McLarty *et al.* 1936
B	B_1	————	K	Twigs	0.00060-0.00120	0.00087-0.00218	Woodbridge 1937
B	A	————	K	Twigs	0.000489-0.001362	0.001122-0.001525	Woodbridge 1937
B	A	————	G	Twigs	0.00059-0.00115	0.00087-0.00150	Woodbridge 1937
B	A	————	K	Fruit	0.0003-0.0008	0.0010-0.0013	Askew 1935
B	A, B_2	————	K	Fruit	0.00036-0.00084	0.00175-0.00761	Askew & Chittenden 1936
B	A	————	K	Fruit	0.000226-0.000454	0.000967-0.002762	McLarty *et al.* 1936
B	B_1	Mar. (F)	I	Fruit flesh	0.00039-0.00112	0.00100-0.00306(Q)	Askew *et al.* 1936
B	B_3	Mar. (F)	L	Fruit	0.00036-0.00079	0.00084-0.00404	Askew & Chittenden 1936a
B	B_1	————	G	Fruit	0.00046-0.00078	0.00122-0.00341	Askew & Thomson 1937
B	A	————	G	Fruit	0.00021-0.00065	0.00050-0.00276	Woodbridge 1937
B	A	————	G	Fruit	0.00039-0.00089	0.0016-0.0020	Chittenden & Thomson 1938
B	A	————	G	Fruit without seeds	0.00040-0.00097	0.00090-0.00341	Askew & Thomson, 1939
B	B_1 (?)	————	K, K_1	Fruit	0.000248	0.000462-0.000543	Heinicke *et al.* 1942
Mn	A	————	J	Basal leaves on current growth	0.0005	0.00549-0.01246	Epstein & Lilleland 1942
Cu	A, B_1 B_2	————	K	Uppermost 4 leaves	0.0001-0.0004	0.00032-0.0012	Dunne 1938
Zn	A, B	Sept.-Oct.	K	Leaves (of apical 6"-8")	0.0004-0.0054	0.0004-0.0080	Chandler *et al.* 1934
Zn	A, B	Sept.-Oct.	K	Stems (apical 6"—8")	0.0004-0.0028	0.0016-0.0080	Chandler *et al.* 1934
APRICOT (*Prunus armeniaca*)							
B	A	Oct.	J	Leaves	————	0.0052	0.0082 Eaton, F. M., 1935
B	B_1, B_3	Dec. (F)	I	Leaves	0.00125	0.00320-0.00405 (Q)	———— Askew & Williams 1939
B	D	June	K	Leaves	0.00025-0.00068	0.00216-0.00295 (Q)	———— Fitzpatrick & Woodbridge 1941
B	A	————	K	Leaves	————	0.0049	0.0118 Eaton *et al.* 1941
B	A	Oct.	J	Twig bark	————	0.0038	0.206 Eaton, F. M., 1935
B	A	Oct.	J	Twig wood	————	0.0023	0.0082 Eaton, F. M., 1935

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of elements in dry matter, unless otherwise indicated: Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
APRICOT (*Prunus armeniaca*)—continued									
	B	A	————	K	Twig bark	————	0.0022	0.0063	Eaton *et al.* 1941
	B	A	————	K	Twig wood	————	0.0005	0.0027	Eaton *et al.* 1941
	B	A	Spring	K	Twigs	0.00045	0.00200-0.00208	————	Fitzpatrick & Woodbridge 1941
	B	B_1, B_3	Dec. (F)	I	Fruit	0.00057	0.00345-0.00465 (Q)	————	Askew & Williams 1939
	B	A	————	K	Fruit flesh	————	0.0041	0.0441	Eaton *et al.* 1941
	B	A	————	K	Fruit shell	————	0.0003	0.0052	Eaton *et al.* 1941
	B	A	————	K	Seeds	————	Trace	0.0085	Eaton *et al.* 1941
	Zn	A, B	Sept. Oct.	K	Leaves (of apical 6"—8")	0.0024-0.0030	0.0019-0.0031	————	Chandler *et al.* 1934
	Zn	A, B	Sept.-Oct.	K	Stems (apical 6"—8")	0.0007-0.0009	0.0011-0.0034	————	Chandler *et al.* 1934
ARTICHOKE (*Cynara scolymus*)									
	B	D	Mar.	I	Leaf laminae	0.0038	0.0112	0.0236-0.1358	Eaton 1944
	B	D	Mar.	I	Plant	0.0028	0.0087	0.0155-0.0817	Eaton 1944
ASPARAGUS (*A. officinalis*)									
	B	D	May-Oct.	I	Tops	0.0043-0.0055	0.0054-0.0244	0.0175-0.0288	Eaton 1944
	B	D	May	I	Roots	0.0013	0.0016-0.0030	0.0059	Eaton 1944
AVOCADO (*Persea americana*)									
	B	E	————	K	Leaves	0.000276-0.000818 (M)	0.001133-0.003757 (M)	————	Haas 1943
	B	E	————	K	Leaves	0.000626-0.001200 (M_1)	0.000975-0.002000 (M_1)	————	Haas 1943
	Cl	A	Jan.-May	G	Leaves	————	0.09-0.032.	0.54-1.34	Haas 1929
	Cl	A	————	G	Fruit pulp (stem half)	————	0.014-0.090	0.102-0.301	Haas 1936a
	Cl	A	————	G	Fruit pulp (tip half)	————	0.013-0.060	0.097-0.267	Haas 1936a
	Cl	A	————	G	Fruit skin (stem half)	————	0.022-0.190	0.127-1.280	Haas 1936a
	Cl	A	————	G	Fruit skin (tip half)	————	0.024-0.110	0.096-1.000	Haas 1936a
BARLEY (*Hordeum vulgare*) [*see also* Cereals]									
	B	D	July	I	Grain	————	0.0003-0.0011	0.0012-0.0051	Eaton 1944
	B	D	July	I	Plant	————	0.0015-0.0078	0.0219-0.1111	Eaton 1944
BEET (*Beta vulgaris*) [*see also* Chard, Mangold, Sugar Beet.]									
	B	D	Aug.	I	Leaf laminae	0.0052	0.0104-0.0370	0.0637-0.1263	Eaton 1944
	B	A, B_1	————	J	Roots	0.00111-0.00123	0.00115-0.00137	————	Brandenburg 1932
	B	A, B_1	————	J	Roots	0.0084-0.0503 (N)	0.0603-0.0771 (N)	————	Brandenburg 1932
	B	D	Aug.	I	Roots	0.0033	0.0016-0.0046	0.0044-0.0082	Eaton 1944
	B	D	Aug.	I	Plant	0.0038	0.0043-0.0138	0.0198-0.0386	Eaton 1944

BLACK CURRANT (*Ribes nigrum*)								
	K	B_I	Sept.	I	Leaves	0.78	0.91-1.06	Wallace & Osmond 1941
	Mg	B_I	July	I	Leaves	0.11-0.43	0.26-0.45	Wallace 1940a
BRUSSELS SPROUT (*Brassica oleracea* var.)								
	B	B_1, D	Oct.	I	Leaves	0.0005-0.0014	0.0023-0.0049 (Q)	Maier 1944
CABBAGE (*Brassica oleracea*)								
	N	A	———	J	Petioles (2% acetic acid extract)	0.0078 (O)	0.0518 (O)	Carolus 1938; Carolus *et al.* 1938
	Mg	A	———	J	Leaf bases	0.092	0.165-0.178	Carolus 1935
	Mg	A	———	J	Leaf tips	0.037	0.076-0.119	Carolus 1935
	Mg	A	———	G	Upper leaves (2% acetic acid extract)	0.0015-0.0018 (O)	0.0060 (O)	Carolus 1936
	Mg	A	———	G	Lower leaves (2% acetic acid extract)	0.0012 (O)	0.0045-0.0068 (O)	Carolus 1936
	Mg	A	———	G	Stems (2% acetic acid extract)	0.0036 (O)	0.0060-0.01666 (O)	Carolus 1936
	Mg	A, B_2	Seedling stage	G, I	Tops	0.43	0.56-0.57	Parbery 1937
	B	B_1, D	Nov.	I	Leaves	0.0005-0.0018	0.0022-0.0038	Maier 1944
	B	D	Apr.	I	Outer leaves	———	0.0016-0.0204	0.0440-0.1152 Eaton 1944
	B	D	Apr.	I	Inner leaves	———	0.0022-0.0055	0.0060-0.0110 Eaton 1944
	B	D	Apr.	I	Plant	———	0.0021-0.0081	0.0263-0.0713 Eaton 1944
CACAO (*Theobroma cacao*)								
	K	D	———	J	Leaf laminae	1.85	2.81-3.27	——— Hardy 1937
	K	A, B_1	———	J	Leaf laminae	0.55-1.94	1.43-1.68 (Q)	——— Hardy 1937
CALENDULA (*C. officinalis*)								
	B	D	Apr.	I	Leaves	———	0.0033-0.0272	0.0715-0.2106 Eaton 1944
	B	D	Apr.	I	Plant	———	0.0019-0.0121	0.0324-0.1025 Eaton 1944
CARPET GRASS (*Axonopus affinis*)								
	P	B_I	Summer	I	Clippings	0.100-0.107	0.157-0.234	——— Blaser & Stokes 1943
	K	B_I	Summer	I	Clippings	0.401	0.366-0.934	——— Blaser & Stokes 1943
CARROT (*Daucus carota*)								
	N	D	———	I	Petioles (2% acetic acid extract)	0.0055 (O)	0.0521-0.0833 (O)	——— Hill 1943
	P	D	———	I	Petioles (2% acetic acid extract)	0.0015-0.0022 (O)	0.0125-0.0250 (O)	——— Hill 1943
	K	D	———	I	Petioles (2% acetic acid extract)	0.054 (O)	0.328-0.647 (O)	——— Hill 1943
	B	D	Apr.-Sept.	I	Leaf laminae	———	0.0036-0.0204	0.0324-0.1244 Eaton 1944
	B	D	Apr.-Sept.	I	Roots	———	0.0022-0.0064	0.0065-0.0319 Eaton 1944
	B	D	Apr.-Sept.	I	Plant	———	0.0027-0.0116	0.0189-0.0570 Eaton 1944

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated: Showing deficiency symptoms	Without symptoms	Showing toxicity symptoms	Reference
CELERY (*Apium graveolens*)									
	B	A, B_1	Oct.	J	Leaves	0.0015	0.0027-0.0048	———	Maier 1943
	B	D	Mar.	I	Leaflets	0.0020	0.0068-0.0432	0.0720	Eaton 1944
	B	A, B_1	Oct.	J	Crowns	0.0013	0.0019-0.0029	———	Maier 1943
	B	A, B_1	Oct.	J	Roots	0.0022	0.0027-0.0040	———	Maier 1943
	B	D	Mar.	I	Plant	0.0026	0.0063-0.0400	0.0729	Eaton 1944
CEREALS [*see also* Barley, Maize, Milo, Oats, Rice, Rye, Wheat]									
	Mg.	?	Young	?	Plant	0.15-0.51	0.24-0.58	———	van Itallie 1937
CHARD (*Beta vulgaris* var. *cicla*) [*see also* Beet]									
	B	D	Mar.	I	Plant	———	0.0016-0.0139	0.0200	Eaton 1944
CHERRY (*Prunus cerasus* etc.)									
	K	B_1	July	I	Leaves	0.39-1.82	2.06-2.13	———	Boynton 1944
	B	D	Nov.	I	Leaves	0.0014	0.0104	0.0182	Eaton 1944
	B	D	Nov.	I	Stems	0.0002	0.0023	0.0085	Eaton 1944
	B	D	Nov.	I	Roots	0.0002	0.0054	———	Eaton 1944
	Mn	A	———	J	Basal leaves on current growth	0.0021	0.00539-0.00717	———	Epstein & Lilleland 1941
CITRUS [*see also* Grape-fruit, Lemon, Orange]									
	Mg	A	Autumn	L	Leaves	0.0251-0.0469	0.103-0.184	———	Bahrt & Hughes 1937
	B	A, B_1	———	K	Leaves	———	0.0031-0.0177	0.0325-0.1162	Scofield & Wilcox 1931
	Mn	A	———	K (?)	Leaves	0.00037-0.00049	0.0014-0.0020	———	Chapman *et al.* 1939
	Zn	A	———	L	Leaves	0.00038-0.00117	0.00078-0.00160	———	Gaddum *et al.* 1937
	Zn	A	———	L	Twigs & petioles	0.00051-0.00093	0.00054-0.00271	———	Gaddum *et al.* 1937
	Zn	—	———	—	Young leaves	0.0005-0.0020	usually >0.0020	———	Grimmett 1938
	Na	D	———	K	Older leaves	———	0.026	0.88	Chapman & Brown 1943
COTTON (*Gossypium hirsutum*)									
	B	D	Nov.	I	Leaves	0.0016	0.0187-0.0306	0.0522-0.1625	Eaton 1932, 1944
	B	D	Nov.	I	Stems and roots	0.0015	0.0024-0.0032	0.0033-0.0060	Eaton 1932, 1944
COWPEA (*Vigna sinensis*)									
	K	A	———	J	Stems and petioles (?) (2% acetic acid extract)	0.0041 (O)	0.4980 (O)	———	Carolus 1936
	B	D	Aug.	I	Leaves	———	0.0032-0.0119	0.0404-0.1132	Eaton 1944
	B	D	Aug.	I	Plant	———	0.0027-0.0070	0.0195-0.0573	Eaton 1944
FIELD BEAN (*Vicia faba*)									
	K	A	May-June	J	Upper leaves	0.58-1.19	1.05-1.75	———	Large 1945a

FIG (*Ficus carica*)									
	B	D	Nov.	I	Leaves	0.0015	0.0404	0.0722-0.1296	Eaton 1944
	B	D	Nov.	I	Roots	0.0010	0.0028	0.0063	Eaton 1944
FLAX (*Linum usitatissimum*)									
	Ca	A	———	J	Tops	0.20-0.45	0.37-0.52	———	Millikan 1944
FRENCH BEAN = KIDNEY BEAN (*Phaseolus vulgaris*)									
	B	D	Aug.	I	Leaves	———	Trace	0.0151-0.1733	Eaton 1944
	B	D	Aug.-Sept.	I	Plant	———	0.0006-0.0012	0.0085-0.0997	Eaton 1944
	Mn	B_1	———	I	Plant	———	0.0032-0.0068	0.0207-0.1340	Parbery 1943
GOOSEBERRY (*Ribes grossularia*)									
	K	B_1	June	I	Leaves of terminal shoots	0.534-0.880	1.476-1.670	———	Wallace 1928a
	K	B_1	July	I	Older leaves of current season's shoots	0.80-0.91	1.93-4.24	———	Wallace 1940a
	K	B_1	June	I	Stems of terminal shoots	0.473-0.529	0.920-1.055	———	Wallace 1928a
	K	B_1	June	I	Fruit	0.965-1.202	1.170-1.734	———	Wallace 1928a
	Mg	B_1	July	I	Older leaves of current season's shoots	0.17-0.37	0.25-0.31	———	Wallace 1940
GRAPE (*Vitis* spp.)									
	K	B_1	———	I	Leaf laminae	0.27-0.59	0.45-0.78	———	Askew 1944
	K	A	Sept.	K	Leaves	0.25-0.27	0.56-0.61 (Q)	———	Boynton 1945b
	K	B_1	———	I	Fruit	0.53-1.09	0.69-1.08	———	Askew 1944
	B	B_1	Aug.	K	Mature leaves	0.0006-0.0024	0.0018-0.0054	———	Scott 1941
	B	B_1	———	I	Leaf laminae	0.00055-0.00191	0.00291-0.00418	———	Askew 1944
	B	D	Sept.-Nov.	I	Leaves	0.0038-0.0086	0.0250-0.0267	0.0926-0.1804	Eaton 1944
	B	D	Nov.	I	Stems	0.0028	0.0050	0.0050-0.0155	Eaton 1944
	B	B_1	———	I	Fruit	0.00044-0.00088	0.00150-0.00339	———	Askew 1944
	Cu	A	Apr. (F)	K	Mature leaves	0.00012-0.00018	0.00026-0.00039	———	Teakle *et al.* 1943
	Cu	A	Dec. (F)	K	Leaves	0.00021-0.00054	0.00075-0.00099	———	Teakle *et al.* 1943
	Cl	A	———	K	Leaves	———	0.04	1.07-3.84	Ravikovitch & Bidner 1937
	Cl	A	———	K	Fruit	———	0.09	0.29-1.50	Ravikovitch & Bidner 1937
GRAPEFRUIT (*Citrus paradisi*) [*see also* Citrus]									
	Mg	A	Oct.	J	Leaves	0.122-0.228	0.013-0.017	———	Fudge 1939
	B	A	———	K	Leaves	———	0.0128-0.0468 (Q)	0.0747-0.1522	Scofield & Wilcox 1931
	B	B_1	Sept.	I	Leaves of spring growth	———	0.009-0.023	0.028-0.037	Fudge 1943
	B	D	———	J	Leaves	0.00050-0.00112	0.00330-0.01008	———	Roy 1943
	Mn	A, B_3	———	K	Leaves	0.00088-0.00105	0.00347	———	Levitt & Nicholson 1941
	Zn	B_1	———	J	Leaves	0.0004-0.0006	0.0008-0.0010	———	McGeorge 1939

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated: Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
JERUSALEM ARTICHOKE (*Helianthus tuberosus*)									
	B	D	July	I	Dead leaves	———	0.0171	0.0519-0.1590	Eaton 1944
	B	D	July	I	Plant	———	0.0028	0.0098-0.1001	Eaton 1944
KIDNEY BEAN [*see* FRENCH BEAN]									
LEMON (*Citrus limonia*) [*see also* Citrus]									
	K	D	Oct.	I	Leaves	0.05-0.39	1.55-2.62	———	Chapman & Brown 1943
	B	A, B_1	———	J (?)	Leaves	0.0266-0.1400	0.0019-0.0076	———	Kelley & Brown 1928
	B	A	———	K	Leaves	———	0.0038-0.0380 (Q)	0.0460-0.0922	Scofield & Wilcox 1931
	B	D	———	K	Leaves	0.0020-0.0040	0.0152-0.0200	———	Chapman and Brown 1943
	B	D	Sept.	I	Leaves	———	0.0061	0.0314-0.1232	Eaton 1944
	Mn	A, E	———	J	Leaves	0.0002-0.0004	0.0014-0.0075	———	Chapman *et al.* 1939
LETTUCE (*Lactuca sativa*)									
	B	D	Aug.	I	Leaves	———	0.0027-0.0043	0.0070-0.0847	Eaton 1944
	B	D	Aug.	I	Plant	———	0.0025-0.0038	0.0058-0.0535	Eaton 1944
LUCERNE (*Medicago sativa*)									
	K	A	———	J	Leaves	0.14	0.83	———	Davies 1940
	K	A	———	J	Stems	0.9	0.8	———	Davies 1940
	B	A	———	G or H	Leaves	0.000366-0.000950	0.00145-0.00322	———	McLarty *et al.* 1937
	B	B_1	Late summer	I	Leaves	0.0007-0.0014	0.0012-0.0038	———	Dregne & Powers 1942
	B	D	Apr.-Sept.	I	Leaves	———	0.0028-0.0654	0.0516-0.0996	Eaton 1944
	B	D	Apr.-Sept.	I	Stems	———	0.0011-0.0055	0.0028-0.0094	Eaton 1944
	B	D	Apr.-Sept.	I	Roots	———	0.0020-0.0047	0.0052-0.0058	Eaton 1944
	B	D	Apr.-Sept.	I	Plant	———	0.0016-0.0353	0.0247-0.0397	Eaton 1944
LUPIN (*Lupinus hartwegi*)									
	B	D	Apr.	I	Plant	———	0.0027-0.0096	0.0367-0.0815	Eaton 1944
MAIZE (*Zea mays*) [*see also* Cereals]									
	K	B_1	Aug.	I	Lower stems	0.029-0.100 (P)	0.334-0.595 (P)	———	Pettinger 1931
	K	A	Early	H	Plant	0.88-1.37	1.99-4.54	———	Stanford *et al.* 1942
	Ca	D	25 days	I	Tops	0.30	0.76-0.80	———	Marsh & Shive 1941
	Mg	B_1	———	I	Leaf blades	0.07	0.20	———	Jones 1929
	Mg	B_1	———	I	Leaf sheaths	0.07	0.24	———	Jones 1929
	Mg	B_1	———	I	Stem nodes	0.06	0.21	———	Jones 1929
	Mg	B_1	———	I	Stem internodes	0.04	0.10	———	Jones 1929
	B	D	Oct.	J	Leaves	———	0.0027-0.0072	0.0179	Eaton 1944
	B	D	25 days	I	Tops	0.0001-0.0002	0.0005-0.0008	0.0025	Marsh & Shive 1941
	B	D	June	I	Plant	———	0.0011-0.0032	0.0123-0.0727	Eaton 1944
	B	D	———	I	Plant	0.0003-0.0019 (T)	0.0019-0.0151 (T)	———	Reeve & Shive 1943

MANGOLD (*Beta vulgaris* var.) [*see also* Beet]								
B	A	———	J	Leaves	0.0007-0.0021	0.0020-0.0049	———	Brandenburg 1939
B	A	———	J	Roots	0.0016	0.0017	———	Brandenburg 1939
MILO (*Sorghum vulgare*) [*see also* Cereals]								
B	D	Nov.	I	Leaves	———	0.0016-0.0138	0.0625-0.2009	Eaton 1944
B	D	Nov.	I	Stalks & sheaths	———	0.0011	0.0023-0.0261	Eaton 1944
B	D	Dec.	I	Plant	———	0.0002	0.0007-0.0189	Eaton 1944
MUSKMELON (*Cucumis melo*)								
B	D	Aug.	I	Leaves	———	0.0037-0.0223	0.0923-0.3875	Eaton 1944
B	D	Aug.	I	Plant	———	0.0028-0.0147	0.0530-0.2220	Eaton 1944
MUSTARD (*Brassica* sp.)								
B	D	Jan.	I	Plant	———	0.0049-0.0080	0.0108-0.0205	Eaton 1944
OATS (*Avena sativa*) [*see also* Cereals and Table XV].								
K	B_1	Before maturity	I	Leaves	0.295-0.444	1.150	———	Lundegårdh 1932
Ca	C	Flowering	K	Tops	0.11-0.14	0.26	———	Atterberg 1901
Ca	D	Harvest	K	Straw	0.10-0.14	0.36-0.64	———	Atterberg 1901
Mg	A, C	Apr.-May	I	Plant (?)	0.10-0.39	0.18-0.52	———	van Itallie 1936
Mg	C	4-6 leaf stage	I	Plant (?)	0.073-0.255	0.127-0.286	———	van Itallie 1937
B	D	July	I	Grain	———	0.0013-0.0019	0.0043-0.0419	Eaton 1944
B	D	July	I	Plant	———	0.0006-0.0064	0.0283-0.1622	Eaton 1944
B	C	Starting to head	I	Plant	———	0.0015-0.0050	0.0054-0.0400+	Jones & Scarseth 1944
Mn	A	———	G or H	Leaves	<0.0015-0.0402	0.0032-0.0240	———	Lundegårdh 1931, 1932
Mn	B_1	———	J	Leaves	0.0005	0.0012	———	Albert 1932
Mn	A	Flowering	G	Tops (?)	0.00102-0.00143	0.00204-0.00820	———	Samuel & Piper 1929
Mn	E	Just after flowering	K	Tops	0.00062-0.00127	0.00139-0.0111	———	Samuel & Piper 1929
Mn	C	11 weeks	I	Plant	0.00105	0.0064-0.0140 (Q)	———	Samuel & Piper 1928
Mn	C	Harvest	I	Plant	0.0009	0.0025-0.0054 (Q)	———	Samuel & Piper 1928
Mn	C	Flowering	I	Plant	0.00048-0.00099	0.00089-0.00567	———	Piper 1931
Cu	B_1	Harvest	I	Straw	0.000310-0.000506	0.000525-0.000699	———	Rademacher 1937
Cu	E	Harvest	I	Tops	0.00009-0.00025	0.00011-0.00088	———	Piper 1942
Cu	B_1	Harvest	I	Plant (?)	0.00019	0.00019-0.00037	———	Teakle *et al.* 1940
OLIVE (*Olea europaea*)								
B	A, B_2, C	———	K, L	Leaves	0.0007-0.0013	0.0014-0.0180 (Q)	0.0268	Hansen 1945
ONION (*Allium cepa*)								
B	D	Apr.-Sept.	I	Leaves	———	0.0029-0.0044	0.0091-0.1578	Eaton 1944
B	D	Apr.-Sept.	I	Roots	———	0.0023-0.0028	0.0021-0.0346	Eaton 1944
B	D	Apr.-Sept.	I	Plant	———	0.0027-0.0033	0.0058-0.1186	Eaton 1944
ORANGE (*Citrus aurantium, sinensis* etc.) [*see also* Citrus]								
K	D	Oct.	J	Leaves	0.46-0.55	1.71-2.72	———	Cullinan *et al.* 1939
K	A	———	K	Leaves	0.59-0.93	1.5-2.44	———	Cullinan *et al.* 1939
K	D	Oct.	I	Leaves	0.06-0.25	2.05-3.45	———	Chapman & Brown 1943
Ca	D	Sept.	J	Leaves	0.14-0.20	1.48	———	Reed & Haas 1923
Ca	D	Sept.	J	Shoots	0.23-0.28	1.17	———	Reed & Haas 1923
Ca	D	Sept.	J	Trunk	0.62-0.66	0.63	———	Reed & Haas 1923

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated: Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
ORANGE (*Citrus aurantium, sinensis* etc.) [*see also* Citrus]—continued									
	Ca	D	Sept.	J	Roots	0.42	0.50	———	Reed & Haas 1923
	Ca	D	Sept.	J	Rooflets	0.29-0.36	2.00	———	Reed & Haas 1923
	Mg	A	Nov.	K	Mature leaf laminae	0.026-0.128	0.172-0.518	———	Parbery 1935
	S	C, D	———	K	Young terminal leaves	0.075-0.096	0.189-0.260	———	Chapman & Brown 1941a
	S	C, D	———	K	Old leaves	0.120-0.129	0.220-0.320	———	Chapman & Brown 1941a
	S	A, D	———	I	Twigs	0.014	0.029	———	Haas 1936
	S	A, D	———	J	Trunk bark	0.031-0.036	0.017-0.077	———	Haas 1936
	S	A, D	———	I	Rootlets	0.066	0.079	———	Haas 1936
	B	A	———	K	Leaves	———	0.0035-0.0522	0.0558-0.1062	Scofield & Wilcox 1931
	B	A, B_1	———	K	Leaves	———	0.0021-0.0087	0.0463-0.1679	Kelley & Brown 1928
	B	A	May	G	Leaves	0.00043-0.00128	0.00145-0.00184	———	Morris 1938
	B	A, B_1	Jan.-July	I	Young and mature fruit	0.00049-0.00090	0.00063-0.00258	———	Morris 1938
	Mn	D	———	J	Leaves	0.0007-0.0010	0.0018-0.0020	———	Chapman *et al.* 1939
	Mn	A, B_3	———	K	Leaves	0.00044-0.00111	0.00208-0.00294	———	Levitt & Nicholson 1941
PARSLEY (*Petroselinum hortense*)									
	B	D	Mar.	I	Plant	———	0.0016-0.0388	0.0588-0.0890	Eaton 1944
PEA (*Pisum sativum*)									
	P	D	Flowering	I	Stems (2% acetic acid extract)	0.0015.-0.0046 (O)	0.0156-0.0500 (O)	———	Hill 1943
	K	A, B_1	———	H, I	Foliage	0.21-0.25	0.50	———	Brickley 1943
	K	A	———	J	Lower stems (2% acetic acid extract)	0.004-0.033 (O)	0.500 (O)	———	Carolus 1938. Carolus *et al.* 1938
	K	D	Flowering	I	Stems (2% acetic acid extract)	0.218-0.381 (O)	0.762 (O)	———	Hill 1943
	B	D	May	I	Leaves	———	0.0016-0.0212	0.0609-0.1452	Eaton 1944
	B	D	Mar.-May	I	Plant	———	0.0016-0.0064	0.0110-0.0867	Eaton 1944
	Mn	A	Harvest	J	Seeds	0.00037-0.00050	0.00037-0.00075	———	Löhnis 1936
	Mn	A	Harvest	K	Seeds (different parts)	0.0002-0.0005	0.0004-0.0015	———	Glasscock & Wain 1940
	Mn	B_3, C	Harvest	I, L	Seeds	0.00122-0.00217	0.00160-0.00264	———	Walsh & Cullinan 1945
PEACH *Prunus persica*)									
	K	D	Oct.	J	Leaves	0.46-0.55	1.71-2.72	———	Cullinan *et al.* 1939
	K	A	———	K	Leaves	0.59-0.93	1.50-2.44	———	Cullinan *et al.* 1939
	K	B_1	Late summer	I	Leaves from middle of current season's growth	0.64-1.95	2.05-2.82	———	Cullinan & Waugh 1940

K	A	Summer	K	Leaves from middle of current season's growth	0.50-0.84	1.26-2.78 (Q)	———	Cullinan & Waugh 1940
K	B_1	———	J	Leaves	0.59-1.35	1.58-2.65	———	Cullinan & Batjer 1943
K	D	Sept.	I	Stems (apical 6"—acetate buffer extract)	0.0200-0.1100 (O)	0.1125-0.5500 (O)	———	Davidson & Blake 1938
Ca	D	Sept.	I	Stems (apical 6"—acetate buffer extract)	0.0070-0.0175 (O)	0.0300-0.0525 (O)	———	Davidson & Blake 1938
B	D	Nov.	I	Leaves	———	0.0017-0.0081	0.0170	Eaton 1944
B	D	Nov.	I	Stems	———	0.0007-0.0044	0.0138	Eaton 1944
B	D	Nov.	I	Roots	———	0.0002-0.0053	0.0192	Eaton 1944
Mn	A	June-July	G	Mature basal leaves on current growth	0.00055-0.00193	0.00177-0.03246	———	Epstein & Lilleland 1942
Zn	A, B	Sept.-Oct.	K	Leaves (of apical 6"—8")	0.0006-0.0015	0.0006-0.0043	———	Chandler *et al.* 1934
Zn	A, B	Sept.-Oct.	K	Stems (apical 6"—8")	0.0005-0.0012	0.0011-0.0050	———	Chandler *et al.* 1934
As	A	Summer	K	Leaves		0.00009-0.00013	0.00013-0.00052	Lindner 1943
PEANUT (*Arachis hypogaea*)								
P	D	———	I	Leaves	0.01 (M)	0.02-0.04 (M)	———	Burkhart & Collins 1942
K	D	———	I	Leaves	0.01 (M)	0.21-0.68 (M)	———	Burkhart & Collins, 1942
Ca	D	———	I	Leaves	0.02 (M)	0.17-0.51 (M)	———	Burkhart & Collins 1942
Mg	D	———	I	Leaves	0.01 (M)	0.10-0.17 (M)	———	Burkhart & Collins 1942
PEAR (*Pyrus communis* etc.)								
K	A	Aug.	J	Leaves from middle of terminal shoots	0.43	1.07	———	Reuther 1941a
Cu	A	June-Oct.	H	Leaves	0.00031-0.00051	0.00056-0.00200	———	Oserkowsky & Thomas 1933
Cu	A	———	H	Leaves	0.00032-0.00067	0.00049-0.0041	———	Oserkowsky & Thomas 1938
Cu	A, B	June-July	H	Wood	0.00012-0.00046	0.00018-0.00116	———	Oserkowsky & Thomas 1938
Cu	A, B	June-July	H	Bark	0.00030-0.00042	0.00037-0.00166	———	Oserkowsky & Thomas 1938
PECAN (*Carya pecan*)								
Zn	A, B	Aug.	K	Leaflets	0.00037	0.00039-0.00167	———	Finch & Kinnison 1933
Zn	A	Oct.	K	Leaves at top of tree	Trace-0.0071	0.0066-0.0202	———	Finch 1936
Zn	A, B	Aug.	K	Petioles	Trace	Trace-0.00100	———	Finch & Kinnison 1933
Zn	A, B	Aug.	K	Shoots	Trace	0.00079-0.00153	———	Finch & Kinnison 1933

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated: Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
PINE (*Pinus* spp.)									
	Mg	A	———	J	Leaves	0.078-0.095	0.115-0.176	———	Němec 1942
	Mg	A	———	J	Wood	0.059-0.133	0.063-0.140	———	Němec 1942
PINEAPPLE (*Ananas sativus*)									
	Zn	A	Various	J	Leaf bases	0.0004-0.0026	0.0016-0.0044	———	Lyman & Dean 1942
	Zn	A	Various	J	Distal parts of leaves	0.0004-0.0026	0.0004-0.0026		Lyman & Dean 1942
	Zn	A	Various	J	Stem growing points	0.0006-0.0096	0.0144-0.0158	———	Lyman & Dean 1942
PLUM (*Prunus domestica* etc.)									
	K	A	July	I	Spur leaf laminae	0.22-0.66	0.77-2.57	———	Wallace 1928b
	K	A	———	H	Leaves	0.22-1.11	1.47-2.00	———	Wallace 1931
	K	A	Aug.-Sept.	J	Leaves from middle of terminal shoots	0.32-1.82	0.84-3.30 (Q)	———	Reuther 1941a
	K	A	———	H	Fruit pulp	0.35-0.97	0.55-1.45	———	Wallace 1931
	Mg	A	Sept.	I	Leaves from base of terminal shoots	0.14	0.18	———	Wallace 1940
	B	A	Oct.	J	Leaves	———	0.0033	0.0176	Eaton, F. M. 1935
	B	A	Oct.	J	Twig bark	———	0.0036	0.0412	Eaton, F. M. 1935
	B	A	Oct.	J	Twig wood	———	0.0011	0.0171	Eaton, F. M. 1935
	Mn	A	———	J	Basal leaves on current growth	0.0015	0.00553-0.00926	———	Epstein & Lilleland 1942
	Cu	A,B_1	———	J	Apical leaves	0.00032-0.000425	0.000717-0.000952	———	Anderssen 1932
POTATO (*Solanum tuberosum*)									
	K	B_1	July	I	Leaves	2.90-3.51	5.85-6.79	———	Jones & Plant 1943
	K	A	July-Aug.	J	Upper leaves	1.2-2.1	2.1-3.8	———	Large 1945
	K	B_1	———	I	Leaves	1.55-3.19	5.19-6.36	———	Nicholas & Jones 1945
	K	A,B_1	———	H	Foliage	0.38-0.44	1.00	———	Brickley, 1943
	Mg	A	May-June	J	Upper leaves	0.122-0.218	0.231-0.296	———	Carolus 1933
	Mg	A	May-June	J	Lower leaves	0.043-0.124	0.159-0.251	———	Carolus 1933
	Mg	B_2	Aug.	I	Leaves	0.10-0.20	0.37-0.40	———	Wallace *et al.* 1942
	Mg	B_1	July	I	Leaves	0.16-0.33	0.40-0.86	———	Jones & Plant 1943
	Mg	B_1	———	I	Leaves	0.22-0.24	0.40-0.78	———	Nicholas & Jones 1945
	Mg	C	———	I	Foliage	0.124-0.287	0.279-0.662	———	Carolus 1934
	Mg	A	May	J	Stems	0.135-0.138	0.163-0.166	———	Carolus 1933
	Mg	B_1	Aug.	I	Stems	0.20-0.30	0.61-0.62	———	Wallace *et al.* 1942
	Mg	A	May	J	Tops	0.065-0.115	0.220-0.290	———	Carolus 1933
	Mg	B_1	———	I	Tubers	0.12	0.13	———	Garner *et al.* 1930
	Mg	C	May	I	Plant	0.069-0.133	0.290-0.495	———	Carolus & Brown 1935

RADISH (*Raphanus sativus*)								
B	D	Feb.-Nov.	I	Leaves	0.0008-0.0033	0.0019-0.0195	0.0086-0.1151	Eaton 1944
B	D	Feb.-Nov.	I	Roots	0.0015-0.0033	0.0013-0.0059	0.0062-0.0183	Eaton 1944
B	D	Feb.-Nov.	I	Plant	0.0022-0.0027	0.0019-0.0134	0.0078-0.0724	Eaton 1944
RED CABBAGE (*Brassica oleracea* var.)								
B	A, B_1	———	J, K	Leaves	0.0007-0.0015	0.0020-0.0030	———	Maier 1944
RED CURRANT (*Ribes sativum*)								
K	B_1	June	K	Leaf laminae	0.24-0.99	0.90-1.59	———	Boresch 1938
K	C	———	K	Leaf laminae	0.35-1.45	0.89-3.16	———	Boresch 1938
RED PEPPER (*Capsicum frutescens*)								
B	D	Oct.	I	Leaves	———	0.0034-0.0118	0.0328-0.0882	Eaton 1944
B	D	Oct.	I	Fruit	———	0.0021	0.0016-0.0046	Eaton 1944
B	D	Oct.	I	Plant	———	0.0019	0.0024-0.0048	Eaton 1944
RHUBARB (*Rheum rhaponticum*)								
K	A	———	J	Petioles (2% acetic acid extract)	0.1080 (O)	0.3980 (O)	———	Carolus 1936, 1938, 1938a
RICE (*Oryza sativa*) [*see also* Cereals]								
S	B_1	Dec.-Jan.	K	Straw	0.053-0.062	0.100-0.118	———	Sen 1938a
S	A, B_1	Harvest	K	Straw	0.049-0.064	0.118-0.138	———	Aiyar 1945
S	B_1	Dec.-Jan.	K	Grain	0.096-0.105	0.114-0.126	———	Sen 1938a
S	A, B_1	Harvest	K	Grain	0.080-0.094	0.115-0.138	———	Aiyar 1945
S	B_1	Sept.	K	Plant	0.034-0.040	0.065-0.125	———	Sen 1938a
RYE (*Secale cereale*)								
Mg	A, C	Apr.-May	I	Plant (?)	0.12-0.34	0.19-0.56	———	van Itallie 1936
Cu	B_1	———	J	Grain	<0.00005	<0.0002	———	Sjollema 1933
SAVOY CABBAGE (*Brassica oleracea* var.)								
B	A, B_1	———	I	Leaves	0.0008	0.0015-0.0035 (Q)	———	Maier 1944
SOYBEAN (*Glycine soja*) [*see also* Tables XIII, XIV]								
Mg	B_1	———	I	Plant	0.30	0.59	———	Garner *et al.* 1930
Mn	E	30 days after germination	I	Leaves	See Table XIII	See Table XIII		Somers & Shive 1942
Mn	E	30 days after germination	I	Roots	,,	,,		Somers & Shive 1942
SPINACH (*Spinacia oleracea*)								
Mn	B_2	Harvest (June)	I	Plant	0.00233	0.00342-0.00600	———	Gilbert *et al.* 1926
Mn	B_2	Harvest (Oct.)	I	Plant	0.00518	0.00561-0.01030	———	Gilbert *et al.* 1926
Mn	A	———	J	Stem & petioles (?) (2% acetic acid extract)	0.0012 (O)	0.0031(O)	———	Carolus 1936
STRAWBERRY (*Fragaria chiloensis, etc.*)								
P	D	Jan.-Feb.	I	Leaves	0.0072-0.0075 (O, M)	0.098-0.320 (O, M)	———	Lineberry & Burkhart 1944
P	B_1	June	I	Crown leaves	0.05-0.09 (M)	0.10-0.18 (M)	———	Lineberry *et al.* 1944

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated: Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
STRAWBERRY (*Fragaria chiloensis, etc.*)—continued									
	P	B_1	June	I	Mature crown leaves	0.19	0.28-0.30	———	Lineberry *et al.* 1944
	P	D	Jan.-Feb.	I	Fruit	0.0020-0.0039 (O, M)	0.0039-0.0112 (O, M)	———	Lineberry & Burkhart 1944
	K	D	Jan.-Feb.	I	Leaves	0.10 (O, M)	0.32-1.00 (O, M)	———	Lineberry & Burkhart 1944
	K	D	Jan.-Feb.	I	Fruit	0.027-0.051 (O, M)	0.107-0.210 (O, M)	———	Lineberry & Burkhart 1944
	Ca	D	Jan.-Feb.	I	Leaves	0.10 (O, M, S.)	0.48-0.70 (O, M, S)	———	Lineberry & Burkhart 1944
	Ca	D	Jan.-Feb.	I	Leaves	0.038 (O, M, R)	0.082-0.138 (O, M, R)	———	Lineberry & Burkhart 1944
	Ca	D	Jan.-Feb.	I	Fruit	0.009 (O, M, S)	0.011-0.032 (O, M, S)	———	Lineberry & Burkhart 1944
	Ca	D	Jan.-Feb.	I	Fruit	0.005 (O, M, R)	0.009-0.020 (O, M, R)	———	Lineberry & Burkhart 1944
	Mg	D	Jan.-Feb.	I	Leaves	0.024-0.040 (O, M)	0.20-0.51 (O, M)	———	Lineberry & Burkhart 1944
	Mg	D	Jan.-Feb.	I	Fruit	0.003-0.008 (O, M)	0.009-0.025 (O, M)	———	Lineberry & Burkhart 1944
	B	D	Mar.	I	Plant		0.0044-0.0113	0.0315-0.0755	Eaton 1944
SUGAR BEET (*Beta vulgaris* var.) [*see also* Beet]									
	K	A	———	J	Leaves	0.43-0.98	0.94-8.00	———	Hale 1945
	Mg	A	———	J	Leaves	0.08-0.20	0.21-1.70	———	Hale 1945
	B	A	———	J	Leaves	0.0004-0.0028	0.0025-0.0052	———	Brandenburg 1939
	B	D	Aug.-Sept.	I	Leaf laminae	0.0019-0.0035	0.0020-0.0426	0.0495-0.1008	Eaton 1944
	B	A	———	J	Leaves	0.0006-0.0013	0.0010-0.0044	———	Hale 1945
	B	B_1	Oct.	I	Roots	0.00111-0.00124	0.00124-0.00135	———	Brandenburg 1932a
	B	A	———	J	Roots	0.0013-0.0014	0.0013-0.0015	———	Brandenburg 1939
	B	A	———	J	Roots	0.035-0.052 (N)	0.053-0.066 (N)	———	Brandenburg 1939
	B	D	Aug. Sept.	I	Roots	0.0006-0.0020	0.0002-0.0028	0.0028-0.0052	Eaton 1944
	B	D	Aug.-Sept.	I	Plant	0.0013-0.0033	0.0010-0.0139	0.0147-0.0354	Eaton 1944
	Mn	A	———	J	Leaves	0.0005-0.0030	0.0007-0.1700	0.125-0.302	Hale 1945
SUGAR CANE (*Saccharum officinarum*)									
	Mn	A (?)	———	K	Leaves	Trace—0.0005	0.003	———	Lee & McHargue 1928
	Cl	A	———	I	Plant	———	10.83 (N)	15.75 (N)	Follett-Smith 1934, 1939
SUNFLOWER (*Helianthus annuus*)									
	B	C	6 weeks	I	Tops	0.0008-0.0023	0.0012-0.0150	———	Tanada & Dean 1942
	B	C	6 weeks	I	Tops	———	0.0012-0.0150	0.0200-0.0360	Tanada & Dean 1942
SWEDE (*Brassica napus*)									
	B	A, B_1	———	J	Leaves	0.0018-0.0029	0.0030-0.0066	———	Brandenburg 1939
	B	A, B_1	———	J	Roots	0.0012-0.0015	0.0018-0.0026	———	Brandenburg 1939

SWEET CLOVER (*Melilotus indica*)									
	B	D	Apr.-Aug.	I	Leaves	———	0.0058-0.0665	0.0602-0.2245	Eaton 1944
	B	D	Apr.-Aug.	I	Plant	———	0.0026-0.0265	0.0264-0.0912	Eaton 1944
SWEET PEA (*Lathyrus odoratus*)									
	B	D	Apr.	I	Leaves	0.0030	0.0190	0.0520-0.1551	Eaton 1944
	B	D	Apr.	I	Seeds	0.0001	0.0018	0.0050-0.0055	Eaton 1944
	B	D	Apr.	I	Plant	0.0032	0.0085	0.0211-0.0664	Eaton 1944
SWEET POTATO (*Ipomoea batatas*)									
	Mg	B_1	———	I	Leaves	0.40	0.71	———	Garner *et al.* 1930
	Mg	B_1	———	I	Tubers	0.06	0.06	———	Garner *et al.* 1930
	B	D	Oct.	I	Tops	0.0016	0.0118	0.0310-0.1410	Eaton 1944
	B	D	Oct.	I	Roots	0.0006	0.0044	0.0020-0.0090	Eaton 1944
	B	D	Oct.	I	Plant	0.0013	0.0098	0.0228-0.1083	Eaton 1944
TEA (*Thea sinensis*)									
	K	A	———	J	Leaves	0.24-0.59	0.66-1.59	———	de Haan & Schoorel 1940
TOBACCO (*Nicotiana tabacum*) [*see also* Table XIV]									
	K	A	Sept.	J	Leaves	2.79-3.72	4.37-5.29	———	Lagatu & Maume 1935e
	Mg	B_1	———	I	Leaves	0.08-0.21	0.18-0.65	———	Garner *et al.* 1930
	Mg	B_1	———	I	Stems	0.14-0.24	0.11-0.31	———	Garner *et al.* 1930
	Ca	B_1	———	H, I	Leaves	0.94-1.30	1.33-2.43	———	Garner *et al.* 1930
	B	D	Aug.	I	Leaf laminae		0.0019-0.0261	0.0365-0.0771	Eaton 1944
	B	C.	———	I	Plant	See Table XIV	See Table XIV		Drake *et al.* 1941; Jones & Scarseth 1944
	B	D	Aug.	I	Plant	———	0.0022-0.0117	0.0152-0.0335	Eaton 1944
	Mn	—	———	J	Leaves	———	0.016	0.400-1.100	Jacobson & Swanback 1932
	Mn	—	———	J	Roots	———	0.016	0.317	Jacobson & Swanback 1932
	Mn	C, E	Apr.	K	Plant	———	Trace-0.0334 (Q)	0.0933-1.130	Bortner 1935
TOMATO (*Lycopersicum esculentum*)									
	P	D	50 days	I	Leaves	0.238-0.354	0.420-0.724	———	Kalin 1943
	P	D	50 days	I	Stems	0.200-0.246	0.302-0.546	———	Kalin 1943
	K	D	Apr.-May	I	Leaves	1.04-1.23	1.55-3.76	———	Wall 1939
	K	D	Apr.-May	I	Leaves	0.28-1.44	1.40-2.40	———	Wall 1940a, 1940b
	K	D	Apr.-May	I	Stems	0.86-1.06	1.55-5.30	———	Wall 1939
	K	D	Apr.-May	I	Lower stems	0.16-1.04	1.40-2.32	———	Wall 1940a, 1940b
	K	D	May	I	Fruit	1.52-2.40	4.00	———	Wall 1940a, 1940b
	Mg	A	———	J	Leaf laminae	0.10	0.42	———	Cromwell & Hunter 1942
	B	D	July-Aug.	I	Leaves	———	0.0034-0.0150	0.0253-0.1416	Eaton 1944
	B	D	July	I	Fruit	———	0.0024-0.0027	0.0060-0.0131	Eaton 1944
	B	D	July-Aug.	I	Plant	———	0.0029-0.0078	0.0148-0.0709	Eaton 1944
	B	D	———	I	Plant	0.0014-0.0032 (T)	0.0034-0.0096 (T)	0.0091-0.0415 (T)	Reeve & Shive 1943
	Mn	E	Oct.	I	Leaflets	0.00053-0.00056	0.00697-0.03980	———	Lyon *et al.* 1943
	Mn	E	Harvest	I	Fruit	0.00002	0.00017	———	Lyon *et al.* 1943

Plant spp.	Element	Conditions of growth	Date or stage of development	Unit sampled	Part of plant	Percentage of element in dry matter, unless otherwise indicated: Shewing deficiency symptoms	Without symptoms	Shewing toxicity symptoms	Reference
TOMATO (*Lycopersicum esculentum*)—continued									
	Zn	E	Oct.	I	Leaflets	0.00144-0.00234	0.00269-0.00298	———	Lyon *et al.* 1943
	Zn	E	Harvest	I	Fruit	0.00006	0.00019	———	Lyon *et al.* 1943
TUNG (*Aleurites* spp.)									
	K	A	Sept.	G	Middle leaves from non-fruiting terminals	0.24-0.64	0.61-1.01	———	Drosdoff & Painter 1942
	K	B_1	———	I	Leaves	0.41-0.74	0.70-0.92	———	Painter & Drosdoff 1943
	Mg	A, B_1	Oct.	K	Leaves	0.05-0.16	0.20-0.35 (Q)	———	Drosdoff & Kenworthy 1944
	Mn	B_1	Aug.	I	Leaves	0.0025-0.0122	0.0322 (Q)	———	Dickey and Drosdoff 1943
	Mn	B_1	July-Oct.	G	Middle leaves from non-fruiting terminals	0.0058-0.0081	0.0638-0.3110	———	Drosdoff 1944
	Cu	A, B	Aug.	J	Leaves	0.00026-0.00031	0.00048-0.00057	———	Drosdoff & Dickey 1943
	Zn	A, B_1	———	I	Leaves	0.00036-0.00062	0.00157-0.00358	———	Gaddum *et al.* 1937
	Zn	A, B_1	———	I	Petioles	0.00037-0.00040	0.00091-0.00284	———	Gaddum *et al.* 1937
TURNIP (*Brassica rapa*)									
	B	D	May	I	Leaves	———	0.0016-0.0213	0.0399	Eaton 1944
	B	A	———	G	Roots	0.00047-0.00169	0.00188	———	Rigg *et al.* 1937
	B	D	May	I	Roots	———	0.0019-0.0065	0.0132	Eaton 1944
	B	D	May	I	Plant	———	0.0017-0.0171	0.0349	Eaton 1944
WALNUT (*Juglans regia*)									
	B	A	———	G	Leaves	0.0360-0.1018	0.0016-0.0112	0.0360-0.1018	Kelley & Brown 1928
	B	A	———	K	Leaves	———	0.0108-0.0378 (Q)	0.0432-0.1088	Scofield & Wilcox 1931
	Mn	A	———	J	Basal leaves of current growth	0.0006-0.0025	0.02111-0.02712	———	Epstein & Lilleland 1942
	Mn	A	June	K, L	Leaves	0.00050-0.00085	0.00350-0.00650	———	Vanselow 1945
	Zn	A	Sept.-Oct.	K	Leaves (of apical 6"—8")	0.0011-0.0022	0.0016-0.0030	———	Chandler *et al.* 1934
	Zn	A	Sept.-Oct.	K	Stems (apical 6"—8")	0.0008-0.0017	0.0024-0.0034	———	Chandler *et al.* 1934
WHEAT (*Triticum vulgare*) [*see also* Cereals]									
	Mg	A, C	Apr.-May	I	Plant (?)	0.23-0.32	0.27-0.46	———	van Itallie 1936
	Mn	A	———	K	Plant	0.0004-0.0010	0.0016-0.0028	———	Gallagher & Walsh 1943
	Cu	B_1	———	J	Straw	0.00085	0.0009-0.0018	———	Sjollema 1933
	Cu	B_1	———	J	Grain	0.00015	0.00030-0.00045	———	Sjollema 1933

NOTES

N.B.—Notes A—E refer to column 3, F to column 4, G—M to column 5 and N—T to columns 7—9.

A. Field observations (plants not subjected to differential nutritional treatments).
B. Trial of different nutritional treatments in the field :
   B_1 by soil application,
   B_2 by injection,
   B_3 by spraying.
C. Pot culture trials with soil.
D. Sand culture trials.
E. Solution culture trials.
F. Observations in the Southern Hemisphere (only noted where time of year is stated).
G. District, orchard or field.
H. Part of orchard or field.
I. Group of plants with similar situation or treatment.
J. Group of plants selected on a basis of symptoms.
K. Plant.
L. Part of plant.
M. Soluble in water.
M_1. Insoluble in water.
N. % in ash.
O. % in fresh matter.
P. % in sap.
Q. Including some plants shewing slight symptoms.
R. Variety Blakemore.
S. Variety Klondike.
T. Read from graphs.

As Table I shews, the ranges of nutrient content for affected and unaffected plants are often fairly sharply separated, or have only a very small overlap. This has led many investigators to suggest limiting values, figures below which will normally correspond with the presence of deficiency symptoms, whereas plants appearing healthy will give higher values (and, *mutatis mutandis*, for toxicity disorders). A number of such limiting values are recorded in Table II; others may be deduced by the reader from the composition ranges given in Table I. A few of the limiting values in Table II relate not to percentages of a nutrient in the plant material, but to ratios of nutrients, where the authority quoted considered that the incidence of symptoms of a deficiency depended on the ratio of the content of the deficient nutrient to that of another nutrient element rather than to the total dry matter. In some instances, the limiting value has been stated on a fresh matter or ash basis.

It has sometimes been suggested that the limiting value for appearance of symptoms of deficiency of one nutrient may be modified in accordance with the supply of another. For instance, Atterberg (1888a) in oats and Ulrich (1942) in the tomato have found lower limiting values for potassium when sodium supply is high than when it is low, and de Vries (1939) found that the pH of the substrate affected the relation between magnesium content and the incidence of magnesium deficiency symptoms.

Table II

Limiting values for nutrient content of plant material, below which the development of deficiency symptoms may be expected, or above which toxicity symptoms may occur.

N.B.—Letters in brackets refer to Notes at end of Table

Plant	Disorder	Date or stage of development	Part of plant	Limiting value (% in dry matter of element in question unless otherwise stated)	Reference
APPLE (*Pyrus malus*, etc.)					
	P deficiency	During growing season	Terminal 5" of twig (acetate buffer extract)	0.01 (H)	Davidson, in Hambidge, 1941
	K deficiency	———	Leaves	0.75-1.00	Reuther & Boynton, 1940; Boynton & Compton, 1945
	K deficiency	———	Leaves	0.70	Batjer & Magness, 1939
	K deficiency	July-Aug.	Terminal shoot leaves	0.83 (A)	Wallace, 1940, 1943; Wallace & Osmond, 1941
	K deficiency	———	Leaves	1.00	Cullinan & Batjer, 1943
	K deficiency	July	Median shoot leaves	1.00 (B)	Boynton *et al.* 1944
	K deficiency	During growing season	Terminal 5" of twig (acetate buffer extract)	0.1 (H)	Davidson, in Hambidge, 1941
	Ca deficiency	During growing season	Terminal 5" of twig (acetate buffer extract)	0.1 (H)	Davidson, in Hambidge, 1941
	Ca deficiency	July-Aug.	Terminal shoot leaves	0.72	Wallace, 1939, 1940a, 1943
	Mg deficiency	July-Aug.	Terminal shoot leaves	0.24 (A)	Wallace, 1939, 1940, 1941, 1943
	Mg deficiency	During growing season	Terminal 5" of twig (acetate buffer extract)	0.006 (H)	Davidson, in Hambidge, 1941
	Mg deficiency	Aug.	Middle shoot leaves	0.25 (C)	Southwick, 1943
	Mg deficiency	Midsummer	Shoot leaves	0.15-0.25	Boynton & Compton, 1945
	Mg deficiency	July	Median shoot leaves	0.20	Boynton *et al.*, 1944
	Mg deficiency	———	Shoot leaves	0.20	Boynton & Burrell, 1944a
	Zn deficiency	———	Leaves	0.0123	Archibald & Wann, 1942
BLACK RASPBERRY (*Rubus occidentalis*)					
	K deficiency	———	Leaves	0.20 (J)	Clark & Powers, 1945
BOYSENBERRY (*Rubus* hyb.)					
	K deficiency	———	Leaves	0.50 (J)	Clark & Powers, 1945
CACAO (*Theobroma cacao*)					
	K deficiency	———	Leaves	$\frac{N}{K_2O}$ ratio 1.0	Hardy, 1937
	K deficiency	———	Leaves	$\frac{K_2O}{CaO}$ ratio 1.0	Hardy, 1937
CARROT (*Daucus carota*)					
	P deficiency	Active growth period	Petioles (2% acetic acid extract)	0.0125 (H)	Hill, 1943
CEREALS (*see also* Maize, Oats)					
	Mg deficiency	4-5 leaf stage	Plant	0.097 (E)	van Itallie, 1936
CHERRY (*Prunus cerasus*, etc.)					
	K deficiency	Midsummer	Shoot leaves	0.75-1.00	Boynton & Compton, 1945
	Zn deficiency	———	Leaves	0.0123	Archibald & Wann, 1942
CITRUS (*Citrus* spp.)	[*see also* Grapefruit]				
	K deficiency	July-Sept.	Spring cycle leaves of fruit-bearing branches (D)	0.2	Chapman & Brown, 1942 1943, 1943a; Chapman, *et al.*, 1944

Plant	Disorder	Date or stage of development	Part of Plant	Limiting value (% in dry matter of element in question unless otherwise stated)	Reference
CITRUS (*Citrus* spp.)	[*see also* Grapefruit]—continued				
	K excess	July-Sept.	Spring cycle leaves of fruit-bearing branches (D)	3.0 (Ca% low)	Chapman & Brown, 1942, 1943
	Mg deficiency	Apr.	Spring flush foliage	0.20 (E)	Fudge, 1942
GRAPEFRUIT (*Citrus paradisi*) [*see also* Citrus]					
	Mg deficiency	Apr.	Leaves of spring growth	0.2 (E, I)	Fudge, 1942b
LUCERNE (*Medicago sativa*)					
	B deficiency	———	Leaves	0.0012 (C)	Dregne & Powers, 1942
MAIZE (*Zea mays*) (*see also* Cereals)					
	K deficiency	———	Plant	$\frac{K}{Ca+Mg}$ equivalent ratio 0.2 (E)	Stanford *et al.*, 1942
MANGOLD (*Beta vulgaris*)					
	B deficiency	———	Leaves	0.0018	Brandenburg, 1939
OATS (*Avena sativa*)	[*see also* Cereals]				
	K deficiency	Maturity	Straw	0.83 (Na low)	Atterberg, 1888a
				0.31-0.32 (Na high)	Atterberg, 1888a
	Ca deficiency	Maturity	Straw	0.072-0.129	Atterberg, 1901
	Mg deficiency	4-5 leaf stage	Plant (?)	0.097 (E)	van Italie, 1937
	B toxicity	Starting to head	Plant	$\frac{Ca}{B}$ ratio 200	Jones & Scarseth, 1944
	Mn deficiency	Flowering	Green parts	0.0014	Samuel & Piper, 1929
	Cu deficiency	Maturity	Tops	0.00010	Piper, 1942
PEA (*Pisum sativum*)					
	K deficiency	Flowering	Stems (2% acetic acid extract ?)	0.25 (H)	Hill, 1943
PEACH (*Prunus persica*)					
	P deficiency	During growing season	Terminal 6″ of twig (acetate buffer extract)	0.01 (H)	Davidson, in Hambidge, 1941
	K deficiency	———	Leaves	1.00 (E)	Cullinan *et al.*, 1939 Cullinan & Batjer, 1942, 1943
	K deficiency	Midsummer	Shoot leaves	0.75-1.00	Boynton & Compton, 1945
	K deficiency	During growing season	Terminal 6″ of twig (acetate buffer extract)	0.1 (H)	Davidson, in Hambidge, 1941
	Ca deficiency	During growing season	Terminal 6″ of twig (acetate buffer extract)	0.01 (H)	Davidson, in Hambidge, 1941
	Mg deficiency	During growing season	Terminal 6″ of twig (acetate buffer extract)	0.006 (H)	Davidson, in Hambidge, 1941
	Zn deficiency	———	Leaves	0.0123	Archibald & Wann, 1942
	As toxicity	———	Leaves	0.0002 (F)	Lindner, 1943
PLUM (*Prunus domestica*)					
	K deficiency	———	Leaves	1.50-2.00 (G)	Boynton, 1942,
	K deficiency	Midsummer	Shoot leaves	0.75-1.00,	Boynton & Compton, 1945
	Zn deficiency	———	Leaves	0.0123	Archibald & Wann, 1942
POTATO (*Solanum tuberosum*)					
	Mg deficiency	———	Tops	0.24	Carolus, 1934; Jones & Brown, in Hambidge, 1941

Plant	Disorder	Date or stage of development	Part of Plant	Limiting value (% in dry matter of element in question unless otherwise stated)	Reference
RED CURRANT (*Ribes sativum*)					
	K deficiency		Leaves	0.90	Boresch, 1938
	Cl toxicity		Leaves	$\frac{K}{Cl}$ ratio 1.0	Boresch, 1938
RICE (*Oryza sativa*)					
	S deficiency		Plant	0.06	Sen, 1938a
SOYA BEAN (*Glycine soya*)					
	B toxicity	Harvest	Plant	0.0050-0.0060	Muhr, 1941
	B toxicity		Plant	0.0200	Hodgkiss *et al.*, 1942
	Mn deficiency		Leaves (expressed sap)	$\frac{Fe}{Mn}$ ratio 2.5	Somers & Shive, 1942
	Mn toxicity		Leaves (expressed sap)	$\frac{Fe}{Mn}$ ratio 1.5	Somers & Shive, 1942
SUGAR BEET (*Beta vulgaris*)					
	K deficiency		Leaves	0.83	Hale, 1945
	Mg deficiency		Leaves	0.18	Hale, 1945
	B deficiency		Leaves	0.00175	Brandenburg, 1939
TOBACCO (*Nicotiana tabacum*)					
	N deficiency		Cured leaves	1.50	Garner *et al.*, 1934
	Ca deficiency		Upper leaves	1.1-1.5	Garner *et al.*, 1930
	Ca deficiency		Leaves	> 1.00	McMurtrey, 1931, 1932
	Mg deficiency		Leaves	0.25	Garner *et al.*, 1930; McMurtrey, 1931, 1932
	B deficiency	Flowering (?)	Plant	$\frac{Ca}{B}$ ratio 1340	Drake *et al.*, 1941
	B toxicity		Plant	$\frac{Ca}{B}$ ratio 1200	Jones & Scarseth, 1944
TOMATO (*Lycopersicum esculentum*)					
	P deficiency		Stem (acetate buffer extract)	0.0022 (H)	Hester, 1941
TUNG (*Aleurites* spp.)					
	K deficiency		Leaf laminae	0.6	Drosdoff & Painter, 1942; Drosdoff, 1943
	Mn deficiency	Early part of season	Leaf laminae from middle of shoot	0.0030	Drosdoff, 1943
	Zn deficiency		Leaf laminae	0.0010	Drosdoff, 1943
WHITE CLOVER (*Trifolium repens*)					
	Mo deficiency		Tops	0.0001	Stephens & Oertel, 1943

NOTES

A. It is claimed that these figures also apply to other fruit plants.

B. McIntosh variety.

C. This value is stated to be *near* the critical level.

D. The leaf samples were taken from a height of 3'—7'.

E. Below this value, symptoms were "marked" or "severe".

F. This value applies only to leaves themselves showing injury.

G. This value applies only to leaves themselves showing *no* injury. If the nutrient content falls below this level other parts of the plant may be expected to show injury.

H. Per cent. of fresh matter.

I. Seedy varieties.

J. These values are quoted as "critical levels" without further explanation, but it appears that they are intended to relate to the development of deficiency symptoms.

Interpretation of the Results of Field Trials.

Next to be considered are those investigations principally concerned with the interpretation of the results of manurial trials. First let us exclude the very numerous experiments in which determinations of total uptake per unit area of ground have been made for the purpose of judging what proportion of the added fertilizers has been absorbed by the plant. These experiments deviate from the practice, with which we in general have to deal, of using the *concentration* of nutrients in the plant material as an index; moreover the determination of uptake is so tiresome a process that it would be impracticable as a routine diagnostic procedure. Some investigators, however, have used the percentage composition of the plant material as an index of the nutritional status of the plots in fertilizer trials, and their work at least implies that such data are relevant to diagnosis of the nutritional requirements of plants of unknown history. They may therefore properly be considered here.

Foremost among these investigations are those of what we may describe as the "foliar diagnosis" school (for general accounts, see Jacob, 1929; Lagatu, 1940; Lagatu and Maume, 1934a, 1937, 1937b; Thomas, 1945; Thomas and Mack, 1940a, 1944a; Hibon, 1944). Lagatu and Maume at Montpellier from 1924 onwards published an extensive series of papers, first on the vine (Lagatu and Maume, 1924, 1924a, 1925, 1926, 1927, 1927a, 1927b, 1927c, 1927d, 1927e, 1928, 1928a, 1929, 1930, 1930d, 1930e, 1932, 1932b, 1933a, 1933b, 1933c, 1934, 1936, 1936a, 1936b, 1936d, 1936e, 1937a, 1937c, 1938, 1938a, 1938b, 1939, 1943; Lagatu *et al.*, 1932; Maume, 1942, 1944; Maume and Dulac, 1945), later on potato (Lagatu and Maume, 1929, 1930a, 1930b, 1930c, 1931, 1932a, 1932c, 1933, 1933a, 1934, 1934b, 1934c, 1935b, 1935c, 1935d, 1937c), tobacco (Lagatu and Maume, 1935, 1935a, 1935e, 1936c) and wheat (Maume and Dulac, 1934, 1934a, 1935, 1935a, 1936, 1936a, 1937, 1938, 1938a, 1942; Maume and Bouat, 1937); some years later, their ideas were adopted by Thomas in Pennsylvania (Thomas, 1929, 1930, 1932, 1934), who applied them to potatoes (Thomas, 1936, 1937, 1938, 1938a; Thomas and Mack, 1938, 1939c, 1939d, 1939f, 1944), maize (Thomas, 1938b; Thomas and Mack, 1939, 1939a, 1939b, 1939c, 1939e, 1943; Thomas *et al.*, 1943, 1944), tomato (Thomas and Mack, 1940, 1941, 1941a, 1941b, 1941c, 1941d, 1943a; Thomas *et al.*, 1943a) and snap bean (Thomas *et al.*, 1942). A feature of the method is that the samples taken for analysis consist of leaves from a strictly defined morphological position—a procedure similar to that proposed by Remy (1903, 1903a) for hops—and similar samples are taken on several occasions during the growing season. An exception to this was made in the case of wheat, the samples for this plant consisting of the entire aerial parts gathered at definite stages of development. In interpreting the results of analysis of these samples, attention was concentrated not on the actual percentages of nutrients in the plant dry matter, but on their ratio. The nitrogen, "potash" and "phosphoric acid" contents were expressed each as a percentage of the total weight (Montpellier) or number of equivalents (Pennsylvania) of the three present in the material, and the proportions of the three bases potassium, calcium and magnesium were expressed in the same way. The nutritional status of the plant was then assessed in the main on the basis of these relative values—though at times the absolute percentages were also taken into account. Sometimes the course of change in the analytical data through the growing season was considered to be of importance; at other times the "centre of gravity" of the relative values for successive samples from the same plot was used in place of the individual values.

These methods were used not only for interpreting the results of fertilizer trials, but also for elucidating the effects of disease, cultivation, irrigation and pruning treatments, and varying weather conditions. In addition, Lagatu and Maume (1935e, 1938a) appear to have used the method on occasion to indicate the cause of deficiency disorders of unknown origin. However, it is primarily as a tool of interpretation that the exponents of "foliar diagnosis" regard their method, and very few examples of their practical application in the field have been published. The point of view adopted seems to be that the "nutrition" of the plant is not governed only by the nutrients in the soil (Thomas and Mack, 1944a), or even by those taken up, but by the whole complex of environmental factors, so that the composition of the leaves and the changes in their composition during the growing season provide the most direct information on the "nutrition" of the plant available; the "foliar diagnosis" data do not themselves supply any information on how the mineral composition may be altered in such a way as to give higher yields (Lagatu and Maume, 1937).

The work of Lagatu and Thomas and their collaborators has proved stimulating to a number of agricultural chemists and plant physiologists, though—apart from Klemen (1931)—no other worker appears to have adopted the methods proposed in just their original form. Sandrock (1931) analysed leaves taken periodically from a defined position on the potato plant in the interpretation of a fertilizer trial. Vinet (Vinet, 1931, 1932, 1932a, 1933, 1934, 1935, 1937, 1938, 1942; Vinet and Lemesle, 1930, 1930a) applied the "*diagnostic foliaire*" of Lagatu and Maume to other fertilizer trials on vines; but soon, instead of periodic sampling of leaves during the growing season he turned to a single sampling of shoot wood during the dormant season—a technique to which he gave the name "*diagnostic ligneux.*" Also, he did not adopt the form of expression in trilinear co-ordinates which characterized the Montpellier work but instead presented his results in the form of simple ratios. Beauchamp's work in Cuba was also influenced by the investigations in Pennsylvania and Montpellier; he was concerned with the interpretation of fertilizer trials with sugar cane (Beauchamp, 1939; Beauchamp and Alvarino, 1940; Beauchamp and Lazo, 1938; Beauchamp *et al.*, 1934, 1935) and potato (Beauchamp 1940, 1942), but instead of the whole leaf material he analysed its alcohol extract ("crude chlorophyll") for the nutrient elements. The work on sugar cane in Mauritius (Halais, 1937; Craig, 1938, 1939, 1940, 1941, 1942; Craig and Halais, 1944; Evans, 1940, 1941) was also influenced by the investigations of Lagatu and Maume; but here again the system of trilinear co-ordinates was abandoned, and the more fruitful approach was adopted of plotting actual percentages of nutrients in plant material against responses to fertilizer application.

Among the many other investigations in which plant analysis has been used primarily to interpret the results of field trials may be mentioned those by Wallace and his collaborators on gooseberry (Wallace, 1928a) and other fruit plants (Wallace and Osmond, 1941), potato (Wallace *et al.*, 1942; Jones and Plant, 1943) and tomato (Jones *et al.*, 1944); by Wagner (1931), Lilleland and his colleagues (Lilleland, 1931; Lilleland and Brown, 1940; Lilleland *et al.*, 1942), Baker (1936, 1941, 1943), Magness *et al.* (1940), Cullinan and Waugh (Cullinan and Waugh, 1940; Waugh and Cullinan, 1941), Reuther (1941), Boynton and his collaborators (Boynton, 1944; Boynton and Burrell, 1944; Boynton and Compton, 1944; Boynton *et al.*, 1941, 1943, 1944; Burrell *et al.*, 1942; Smock and Boynton, 1944), Kidson *et al.* (1943), Wander and Gourley (1943), Waltman (1944) and Southwick and his collaborators (Southwick and Shaw, 1944; Southwick and Smith, 1945) on tree fruits; by Darrow and Magness (1939) on raspberries; by the Trinidad investigators (McDonald, 1934; McDonald and Rodriguez, 1935; Hardy and Rodriguez, 1935; Hardy *et al.*, 1935) on cacao and grapefruit; by Neller (1935) on sorghum, buckwheat and sugar cane; by Němec (1938, 1939) on forest trees; by Gilligan (1939) on sweet potatoes; by Moser (1941, 1941a) on lespedeza, clover and peas; by Martin (1940), Hilgeman *et al.* (1940) and Fudge (1941) on citrus; by Chapman (1941) on rubber; by Olson (1942) on cotton and maize; by Ingram *et al.* (1943) on tomato; by Davies *et al.* (1944) on potatoes; and by Hirst and Greaves (1944) on sugar beet.

Determination of Current Nutrient Requirements.

We will now pass on to that group of diagnostic methods depending on the use of rapid chemical analyses, often called "tissue tests," and finding their principal application in advisory work though also widely used in the interpretation of the results of field trials. The tests have usually been carried out on sap or on extracts of fresh material from organs consisting largely of conducting tissue, the theory behind this being that the fractions estimated were mainly unassimilated materials which had recently entered the plant, and that their concentration thus represented the *current* rate of nutrient intake.

The series of tests most extensively used has been that developed at Purdue University, Indiana, mainly by Thornton, from 1926 onwards (Hoffer, 1926; Thornton, 1932, 1933, 1933a; Thornton *et al.*, 1934; for general accounts of the technique, see also Scarseth, 1941a, 1941b, 1942, 1943). The technique only gave information on the three principal nutrients, and of the nitrogen in the extract only that in the form of nitrate was determined. The original investigations leading to the development of these tests were on maize, and maize has continued to be the principal interest of the Purdue workers (Thornton, 1932, 1933, 1933a; Pettinger and Thornton, 1934; Cook, H.L., 1941, 1941a; Drake, 1941, 1944; Ohlrogge, 1941, 1941a; Vittum, 1941;

Scarseth, 1941, 1943, 1943a ; Scarseth *et al.*, 1943). Other plants studied there include potato (Thornton, 1933a), soybean (Thornton, 1933a; Scarseth, 1941), lawn grasses (Scarseth, 1941; Steckel, 1941), lucerne (Jones, 1941) and tomato (Ingram *et al.*, 1943). Investigators at a number of other centres have made use of the Indiana methods for their own problems. Shaw (1935) and Lilleland and Brown (1939) applied them to fruit tree petioles, Wark (1938, 1939) to cereals and peas, Ulrich (1941) to sugar beet petioles, Olson (1942, 1942a) to maize and cotton and Canadian workers (Atkinson *et al.*, 1944) to tomato, potato and sweet corn. The tests are only very roughly quantitative, and this is recognized in that the results are normally reported only in terms of four or five grades—though in his experiment on cotton Olson attempted to interpret them numerically.

Gilbert and his collaborators (Gilbert, 1926 ; Gilbert and Hardin, 1927 ; Gilbert *et al.*, 1927 ; Gilbert and Smith, 1929) proposed the use of analyses of expressed sap of a number of crop species as a means of control of their nutrition, and suggested several critical values (see Table XII). The sap composition was, however, found to be considerably affected by the weather, and after some years of trial the work appears to have been abandoned. Pettinger (1931) also used expressed sap of maize, and was able to suggest approximate limiting values.

Emmert (1932, 1935, 1935a, 1936, 1941, 1942a) carried out analyses for nitrate-nitrogen, phosphate-phosphorus and potassium, using 2% acetic acid extracts of fresh stems and petioles. The results were expressed numerically, and optimal or normal values were suggested for several crops (see Table XII). In the tomato (1941, 1942a) the optimal values were held to vary with the stage of development of the plant.

Morgan, in Connecticut, has been responsible for another series of tissue tests (1935, 1937). The tests were devised primarily for use on soil extracts, but it was claimed that they could also be applied to plant material extracted with the acetate buffer solution recommended. Morgan's methods have since found application to practical diagnostic work in Eire (Walsh, 1942), among other places.

Carolus (1938) also described a series of tests for the five principal nutrients to be used on 2% acetic acid extracts of plant tissue ; he put forward the view that the concentration of a nutrient in such an extract represented the current balance between its absorption and utilization—where the extract from a poorly growing plant contained a low concentration, the absorption of the nutrient was at fault, while if the concentration was unduly high its utilisation was inadequate. Carolus quoted limiting values for the potato (see Table XII) below which deficiency was to be suspected, and found, like Emmert, that these values changed during the course of development. The techniques proposed by Carolus were adopted by Hill (1943) at Ottawa ; previously (1938) when working at East Malling this investigator had made some use of the methods of Thornton, Emmert and Morgan, but apparently he found the methods developed in Virginia more satisfactory.

Hester (1941) is another worker who has described a system of " tissue tests." Tomato stems were extracted with an acetate buffer solution in a mechanical cocktail mixer ; limiting values for deficiency and normal ranges are given (see Table XII) for the content of nitrate-nitrogen, phosphate-phosphorus, and potassium. Like many other workers, however, Hester recommended comparison of the composition of the best and poorest plants in a field rather than reliance on limiting values.

Some interesting recent investigations in Hawaii, though not involving the use of rapid analytical techniques, have some affinity with those mentioned above in that they are attempts to assess the *current* nutrient needs of the plant with a view to immediate supply of the deficient materials. Work in Hawaii, on both sugar cane and pineapple, has been coloured and complicated by the fact that profitable levels for nitrogen applications vary greatly with the climatic conditions in which the crop is growing ; in sugar cane, excess nitrogen may lead to serious decreases in sugar yield. This has led to a search for an index of assimilatory activity or carbohydrate accumulation, so that the balance between carbohydrate and nitrogen reserves in the plant may be estimated. Clements (1940 ; Clements and Kubota, 1943) suggested that for sugar cane the sugar content of the young leaf sheaths would provide such an index (the " primary index "), while Nightingale (1942) for pineapple used an estimate of leaf colour. Both also analysed samples of selected tissue for the three principal nutrients ; Clements chose the leaf

blades of sugar cane for nitrogen determinations (Clements and Moriguchi, 1942), but preferred the young sheaths for estimating the potassium and phosphorus status of the plant. Nightingale (1942, 1942a) chose the meristematic tissue at the base of the leaves for analysis for all three nutrient elements; only the nitrate fraction of the nitrogen present was, however, determined. The concentrations of nutrients to be desired in the index tissue varied with the stage of development reached. Both Clements and Nightingale have given examples of the practical use of the nutritional indices they propose for the purpose of controlling the application of fertilizers during the development of the crop, and, with the pineapple, anyway, this control is shewn to lead to more economical use of fertilizer. Nightingale's method has been used by Tam and Clark (1943) to follow the course of nitrification in sterilized soil. Borden (1942, 1944) too investigated the use of analysis for determining the nitrogen requirements of sugar cane; among other techniques he tested that of Clements but did not find his "primary index" satisfactory. The total percentage of nitrogen in the whole plant, in the crusher juice and in leaf punch samples did however provide useful indices of nitrogen status; but Borden emphasized the need for caution in applying his results to the practical control of nitrogen nutrition in the field.

Determination of Soil Nutrient Status.

The last group of investigations which we propose to include in this general survey of the use of plant analysis for diagnostic purposes consists of those whose primary intention was the description of *soil* conditions as affecting the plant, and not directly the nutritional status of the plant analysed. The results of such work have been considered to have general relevance to the nutritional status of crops grown on that soil. In many cases, such investigations led up to the survey of a wide range of soils to ascertain the distribution of different levels of nutrition among them.

Some of the work in this field does not even involve any interest in plant nutrition. Remington *et al.* (1929), for instance, have used the iodine content of the potato tuber as an index of the distribution of iodine levels for human nutrition. The selenium content of certain wild plants, notably *Astragalus* spp., has been used to survey parts of the United States for the probability of selenium poisoning of man and domestic animals (Byers *et al.*, 1938; Olson *et al.*, 1942, 1942a); and plant analysis has been widely used to judge the probable incidence of cobalt deficiency (McNaught, 1938; Beeson and Smith, 1944) in cattle. In some of the work on the heathlands of Northern Europe in which plant analysis has been used in surveys for copper, the main interest has been in animal nutrition (Sjollema, 1933; Beck, 1941), for a low copper content in the diet can lead to serious diseases of sheep (enzootic ataxia, "swayback") and cattle ("*Lecksucht*," "falling disease.") Finally we may mention in passing Robinson's (1943) suggestion that analyses of hickory leaves could be used to indicate the abundance of the rare earth metals in the soil.

Let us turn now to those investigations in which information on soil composition was sought mainly on account of its relation to plant nutrition in general. As we have seen, many of the early investigators of the diagnostic use of plant analysis approached the problem from this point of view; but the most important recent work on these lines is that of Lundegårdh (1941), who in his method of "triple analysis" attained a much greater measure of success than any of the earlier workers, while concerning himself principally with the same crop plant—oats—as had been used in many of their investigations. The sample for analysis consisted of all the leaves, was gathered between panicle emergence and flowering, and was analysed for the three principal nutrients. From a very extensive series of field trials covering a large part of Sweden, it was possible to draw curves connecting the nutrient content of the sample with the response obtained to fertilizers; these curves would subsequently enable the probable response on a soil of unknown characteristics to be estimated from analysis of a sample of oat leaves. It was a feature of this work that full account was taken of the interactions among the principal nutrients so that the estimated response to a potassium-containing fertilizer, for instance, was not based solely on the potassium content but was modified according to the phosphorus content found in the leaves.

For many years in Hawaii, analyses of sugar cane crusher juice have been carried out as a supplement to soil analyses (Moir, 1935; Borden, 1936b), for the purpose not only of characteriz-

ing the supply of plant nutrients from the soils of different fields, but also for assisting the interpretation of fertilizer trials and, on occasion, to show what treatments may be needed to improve the current nutrition of the crop. Among other investigations on these lines in relation to the principal nutrients for field crops may be mentioned that of Pierre and Pohlman (1933) on the exuded sap of maize and other Gramineae, and those of Gardner and Robertson (1935), Ulrich (1944) and Brown (1943) on sugar beet petioles. The Purdue University testing methods (see p. 71) have been used for soil survey purposes (Veale, 1942), as also have the tests in current use at Long Ashton Research Station (Jones and Russell, 1945 ; Plant, 1945, 1945a, 1945b).

Following observations (Teakle, Morgan and Turton, 1941 ; Teakle, Thomas and Turton, 1941) on the copper content of a number of crop plants in copper-deficient regions, Teakle (Teakle, 1942 ; Teakle and Turton, 1943) took a large series of samples of clover and cereal leaves from different parts of Western Australia, and analysed them with a view to determining the distribution of areas deficient in the trace elements copper, zinc and manganese. The clover samples were taken in the middle of the flowering period, those of oats at a height of 6-8 ins. Both plants were regarded as suitable for indicating copper and probably zinc requirements ; it was uncertain whether they were suitable for manganese, since manganese did not seem to be deficient in any part of the area covered. For clover samples, characteristic content figures for different levels of copper and zinc deficiency were suggested (Tables XI and XII).

Following a series of fertilizer trials on forest trees (Mitchell 1935, 1939 ; Mitchell and Finn, 1935 ; Mitchell and Chandler, 1939) Mitchell and Chandler were able to develop leaf analysis as a method for surveying the nutrient status of forest soils, particularly in relation to nitrogen. The leaf samples were taken in early autumn. It was claimed that this method of evaluation of the nitrogen-supplying power of the soil was not affected by rainfall, the physical properties of the soil, the age of the trees, or the local climate ; root competition had an effect, however, and a correction factor was proposed. For a number of tree species, limiting values for leaf nitrogen were determined (see Table XII); at localities where the leaf nitrogen content fell below this limiting value, the species could not be expected to succeed in competition with others. These methods were also used to study the nutrition of trees growing under experimental conditions (Finn, 1942, 1942a ; Finn and Tryon, 1942). Robinson and Edgington (1942) also suggested that analysis of the leaves of a forest tree—hickory—should be used to indicate the boron status of the soil on which it was growing.

There have been a number of instances in which samples from deciduous fruit trees have been analysed as a means of survey. Following the discovery that corky-core of the apple was a boron-deficiency disorder, a considerable number of analyses of apple fruits from different parts of New Zealand (N.Z. Dep. sci. industr. Res., 1937 ; Askew and Thomson, 1939) and Australia (Piper, 1936) were analysed for boron with a view to determining whether there were areas in which, although corky-core was at the time unknown, there was a risk of it developing in an unfavourable season. Batjer and Magness (1939) in Maryland made a survey of the potassium content of the leaves in a number of apple orchards, having found in sand culture experiments that maximum growth of the trees was not obtained unless the potassium supply was sufficient to maintain a potassium content of 1.7% in the leaves. The following year a similar survey of peach orchards was carried out (Cullinan and Waugh, 1940). Lilleland and Brown (1941, 1942) in California also surveyed peach orchards for potassium and phosphorus status by analysis of leaves collected in June and July—the period of greatest constancy of composition. Boynton and his collaborators (Boynton and Cain, 1942 ; Burrell and Boynton, 1943 ; Boynton *et al.*, 1944) used leaf analysis in a survey of the nutritional status of apple orchards in the State of New York.

This concludes the account of the main lines of development of diagnostic plant analysis during the last two decades ; that many investigations have been omitted or mentioned only inadequately stands to reason—particular points will be discussed in greater detail in subsequent pages.

THE AIM OF A METHOD OF DEFICIENCY DIAGNOSIS

Before discussing the use of plant analysis for the diagnosis of nutritional deficiencies, it is advisable to attempt a definition of deficiency. From one point of view plant analysis could be regarded as a direct measure of deficiency, for when the nutrient content of the plant is low, the plant is obviously, in a sense, *deficient* in that nutrient. But deficiency is more often considered as involving sub-optimal development of the plant in some respect. Sub-optimal development is not, of course, necessarily ascribable to a nutrient deficiency, and consequently some further criterion has to be sought. The only satisfactory criterion would appear to be response to increased uptake of the deficient nutrient by an improvement in development. Cases have been known, however, where, although a particular nutrient is deficient, increase in its uptake has led to no improvement in development; this may happen in certain types of chlorosis, where the iron is immobilized in the conducting tissue and increased supplies to the roots do not reach the leaves; but such plants will usually respond to direct applications of iron-containing solutions to the leaf surfaces. Another group of doubtful cases which has to be covered by a definition of deficiency is that in which the nutrient applied, though its uptake is increased, does not act directly but by affecting the uptake of other nutrients or by altering growth conditions in some other way; this includes most effects of lime and of sulphur applications to soils. It must therefore be stipulated that cure of the deficiency is a specific function of the deficient element. For the purpose of the present discussion, the following definition will be adopted, since it is brought into relation with practical needs:—

A plant is deficient in a certain element if supplying that element to the plant in a suitable form causes an increase in the yield, this effect being specific to the element in question.

A qualitative diagnosis of deficiency—i.e., a conclusion that the yield of a particular crop will probably be increased by fertilizer treatment—is in practice hardly adequate. What is required by the practical farmer of any method for determining fertilizer requirements is a forecast of the increase in the selling value of the total final product which may be expected as a result of any one of the whole indefinite range of possible fertilizer treatments. This selling value will depend not only upon the weight of whatever part of the plant is gathered for sale, but also on any quality criteria which may be in use.* If such forecasts are available, the farmer is then in a position to compute what treatment, at current fertilizer prices and costs of applying the material, will be likely to give the best return; the forecast and the expected return will inevitably be subject to a measure of uncertainty unless and until weather conditions can be accurately predicted for the whole growing period of the crop, and pests and diseases can be brought under full control. Let us then bear in mind that the provision of such forecasts is the central purpose for which we are studying the potentialities of plant analysis; let us also remember that, in order to be of practical use, a plant analysis technique must not only be able to give such estimates, but they also must be better estimates (that is, deviate less from the observed increase) than those from any other available technique for determining fertilizer requirements.

There is an important distinction among methods for the diagnostic use of plant analysis to determine fertilizer requirements which cannot be kept too clearly in mind. A hint of this distinction has already been introduced into the preceding section, but since it has rarely been recognized it is worth repeating more clearly:—

(1) Many techniques are directed to improving the nutrition, during the course of its later growth, of the crop plant analysed. Though results may affect the fertilizer treatment of subsequent crops, such an application of them is purely incidental.

(2) In other techniques the plants analysed serve only as an index of the state of the soil. There is no thought of remedying any state of unsatisfactory nutrition found in these plants—indeed, it would often be too late to do so—but it is intended to apply the results to improving the fertilizer regime for subsequent crops.

* For fodder crops consumed on the farm, the same considerations of quantity and quality apply.

THEORETICAL

From the statement in the preceding section on the aims of a diagnostic method, it will be apparent that two major relations are involved :

(1) The relation of supply of nutrient to yield.

(2) The relation of supply of nutrient to its concentration in the tissues of the plant.

Each of these aspects covers a complex situation, and would demand a comprehensive discussion, but only certain general principles, in so far as they can be stated, will be considered.

RELATION OF YIELD TO NUTRIENT SUPPLY AND UPTAKE

Two major considerations are concerned here : first, the supply of the nutrient from the rooting medium ; second, the utilization of the element after absorption by the roots. In the first problem are included all the questions of absorption, availability of the element in the soil, the effects of acidity, aeration, and so on. To avoid confusing the main issue such consideration will be left out of account. The second opens up the whole question of the physiology of growth. Only a few simple ideas need however be adumbrated. The utilization of the elements absorbed for growth will evidently depend upon the type of plant considered—whether it is perennial, biennial or annual in habit, whether of unlimited growth or strictly limited in size, whether or not of branching habit. As examples of these types we may cite the fruit tree as a perennial type with branched habit and unlimited growth ; the root crops as biennials with unbranched and determinate growth ; and the cereals as branched and determinate annuals. Other types not falling into these categories, such as the potato and tomato, might also be mentioned. Whatever the type of plant, however, the expansion of the growing system will depend upon the number, location and activity of the meristems or growing points. At germination all plants have only two meristematic regions, at the root and shoot apices, and all development depends upon the continued activity of these, and upon the laying down of secondary points of growth. This activity is conditioned by two sets of factors : (1) the external factors such as light, temperature, water supply and nutrient supply among others, and (2) internal factors, mainly nutritive but including hormones. Although of the external factors only nutrient supply is of immediate relevance, it should be stressed that the rate of laying down of new meristems, as well as of their development, is largely a matter of temperature level and is also affected by other external factors such as light.

With regard to the ' intensity ' level of all these factors, the following generalisation is possible, namely, that for each factor in turn there is an optimum level and that growth is increased if the intensity is brought to this level and decreased if it is raised further. These optima are not fixed, but depend upon all factors simultaneously ; nevertheless in theory one may postulate an optimal concatenation of factors at which development of the plant would be maximal, and that no greater rate could be attained by alteration in the level of any one or more factors. The maximal yield of the plant would then be secured, and would be determined entirely by internal genetic factors.

Assuming then that all external factors including all nutrients except one are maintained at optimal level, then as this is raised growth made will be a function solely of the available amount of this single nutrient, and as the optimum is approached the " maximum possible yield " of the plant will be reached. What will now be the relation of yield to the amount of nutrient available ? Two answers have been proposed : (1) the law of limiting factors originally due to von Liebig (1863) ; and (2) the law of diminishing returns, as exemplified by the views of Mitscherlich (1909). According to the first a linear relation between the yield and the amount of nutrient given is expected,* while the second leads to a curve resembling a hyperbola in form,

* von Liebig's formulation was in very general terms : " Every field contains a *maximum* of one or several, and a *minimum* of one or several, other nutritive substances. It is by the *minimum* that the crops are governed." (*loc. cit.*, p. 213). This does not appear to imply any particular form of the rising limb of the curve connecting yield with nutrient supply, but that Liebig did envisage it as linear is shown by the following quotation : " If we wished, by increasing the phosphoric acid required for the formation of seed, to enable a wheat field yielding an average produce of six grains to give two additional grains, it would be necessary to increase by ⅓rd the whole amount of the phosphoric acid present in the field, and serving for the formation of seed." (*loc. cit.*, p. 126).

with maximum gradient at low nutrient levels and approaching a maximum value. Where the increase of a single nutrient factor in the presence of excess of the others is concerned both field and pot culture experiments confirm this diminishing returns relation. The exact mathematical formulation by Mitscherlich is of no ultimate importance except as a method of interpolation. For each series of increasing doses of a nutrient a " maximum possible yield " is assumed, which will depend upon all the other factors operating ; in practice, approximation to this is established by experiment and holds for the particular experiment only. In the field (without such manurial trials) the maximum possible yield is not known and cannot be predicted. If a diminishing returns relation holds (such as Mitscherlich has assumed), the hope of attaching to each nutrient a specific numerical value stating the increase in yield for each unit of nutrient applied (cwt. per acre or other convenient measure) must be abandoned, since the return will depend upon the level of the nutrient already present. In place of this, on Mitscherlich's formulation of yield relations a value (" *Wirkungsmenge* ") can be stated for the amount of any nutrient necessary to bring the yield to any fraction of the " maximum possible yield". If Mitscherlich is correct in his assumption, these values will be independent of the maximum possible yield, and specific for the nutrient element.

The Mitscherlich relation in its simplest form, then, presupposes the presence in excess of all nutrients except the one " limiting " growth. If two elements are simultaneously increased in constant proportions, the combined effect will be the *product* of the individual effects (Baule, 1918) and the curve relating yield to dosage given becomes sigmoid, the precise form varying according to the relative proportions supplied.

The effects on yield of the simultaneous variation in the supply of more than one nutrient have been represented mathematically in a different way by Maskell and by Balmukand (1928). This has become known as the " Resistance Formula," and presupposes that the reciprocal of the yield is the sum of various terms each proportional to the reciprocal of the quantity of a single nutrient supplied. This formulation has been shewn to apply in practice more successfully than that of Mitscherlich.

The work of Gregory (1937) has shewn that under certain circumstances the relation of yield to simultaneous increase in dosage of two nutrients in constant proportions is represented by a straight line. These results were obtained with nitrogen, phosphorus and potassium manuring of barley. By plotting the yield obtained against the amount of nutrient taken up by the plant, three types of relationship were established : (a) With excess of all nutrients except one, which is given in increasing doses, the relationship of yield to the uptake of the nutrient in minimum is given by a curve of the diminishing returns type ; (b) When yield is plotted against the uptake of one of the nutrients *not in minimum*, a curve of yield rising throughout is obtained ; (c) when the supply of two nutrients increased in a certain fixed proportion, the curve relating yield to the uptake of either nutrient became linear, as indicated above. It was further shewn that in sand culture over a wide range the rate of uptake by the plant of the nutrient in minimum was proportional to the amount of nutrient applied to the sand, so that, for the first approximation, the conclusions derived from the amounts taken up can be extended to the amounts of nutrient available to the plant. It should be noted that in these experiments the nutrient doses were added to the sand at germination, so that the concentration in the medium was falling throughout, and most of the nutrient was absorbed in the stage of early growth prior to flowering. With plants growing in soil these relations are necessarily modified, for supply is continuous, although in annuals such as cereals the plant develops under conditions of falling external concentration.

The bearing of these findings on the main problem of deficiency is very evident. Under certain conditions, namely a certain unique proportion of two nutrients, with increasing dosage the increment in yield is directly proportional to the supply, and an estimate of yield will give direct information as to the amounts of the nutrients in the soil ; only under the particular condition of *balance* of the nutrients, or where one is known to be in minimum, can an estimate of total uptake by the whole plant be a measure of the status of a particular nutrient in the soil. In practice, this precondition presupposes a knowledge of conditions in the soil which is exactly the information which a diagnostic method is expected to provide. This leads directly to the second aspect of the problem.

RELATION OF INTERNAL NUTRIENT CONCENTRATION TO NUTRIENT SUPPLY

A divergence of the discussion is necessary here. It has already been pointed out that the development of the plant is determined by the activity of the meristems, and the laying down of secondary growing points. Now the various nutritive elements differ greatly in their effects in this respect. Without going deeply into the question, it may be stated that these effects all depend upon the part played in metabolism, particularly in protein synthesis, since all cell division depends primarily upon cytoplasmic and nuclear proliferation. As might be expected, then, nitrogen plays the chief part, followed by phosphorus and potassium, to name only the three major nutritive elements.

With a nutrient supply in which all elements except one are maintained at high level, the concentration within the plant of the nutrient in minimum will rise with increasing external supply. In general, the concentration of the element in the plant will depend upon the specific relation of the nutrient to the growth process, the rate of uptake, and the rate of utilization. Thus, with nitrogen deficiency growth remains low, no auxiliary meristems are laid down, but the uptake of other elements such as phosphorus and potassium does not cease and these are therefore present in relatively high concentration in the tissues. The same is true to a less extent with phosphorus deficiency, whereas with potassium deficiency growth does not cease and so the nitrogen concentration does not rise to the same degree. The point to be stressed is that the relative concentration of the nutrient elements in the tissues is no measure of the level of supply of any particular element, but depends upon the total supply of all elements—to a varying degree according to the importance of a particular element in the metabolic processes. In a balanced system of nutrients, at any particular stage of growth the relative concentrations may remain unchanged although the size of the plant, and hence the yield also, rises with increasing dosage of the nutrients. The development of deficiency symptoms, too, gives information as to the relative and not the absolute levels of the nutrient factors.

When development of the plant is depressed by low level of external factors such as water supply or temperature, internal concentration will rise; this is true also when slow development is due to lack of any one of the nutrient elements. This simple relationship elucidates the question of "luxury consumption", and the three types of relation between yield and nutrient supply discussed above.

In considering the changes in internal nutrient concentration through the growing season, the type of plant is of importance. The considerations of yield relations dealt with above relate to the state of affairs at the end of the growing season. This in the case of annual plants only will correspond with the final harvest yield; with biennial and perennial plants the growth cycle will be incomplete and the relations somewhat different. For the sake of simplicity an annual plant, such as a cereal, will be considered.

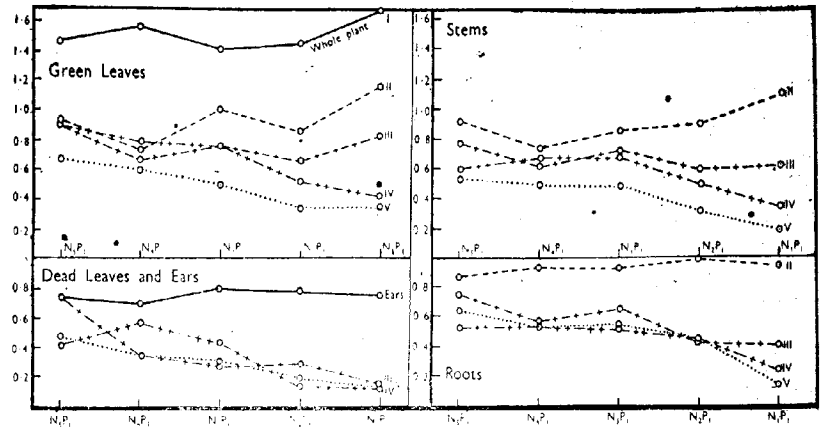
To bring out as clearly as possible the relations of nutrient supply to internal concentration, some data on the growth of barley obtained by Gregory are presented in some detail. The experiment concerned the interaction of nitrogen and phosphorus, was carried out in sand culture, and was designed on a factorial basis. Five levels of deficiency for each nutrient were used, each member of a series receiving one-third that of the preceding. Thus the range of concentrations for nitrogen were as follows (per pot of three plants): N_1, 1215 mg.; N_2, 405 mg.; N_3, 135 mg.; N_4, 45 mg.; N_5, 15 mg. For P_2O_5 one-third of these amounts was given. The suffixes therefore correspond with increasing deficiencies of nutrient. In every case, the total nutrients were added in solution before germination.

The complete interaction experiment may be represented as follows:—

N_1P_1 (1 : 1)	N_1P_2 (1 : 1/3)	N_1P_3 (1 : 1/9)	N_1P_4 (1 : 1/27)	N_1P_5 (1 : 1/81)
N_2P_1 (1/3 : 1)	N_2P_2 (1/3 : 1/3)	N_2P_3	N_2P_4	N_2P_5
N_3P_1 (1/9 : 1)	N_3P_2	N_3P_3 (1/9 : 1/9)	N_3P_4	N_3P_5
N_4P_1 (1/27 : 1)	N_4P_2	N_4P_3	N_4P_4 (1/27 : 1/27)	N_4P_5
N_5P_1 (1/81 : 1)	N_5P_2	N_5P_3	N_5P_4	N_5P_5 (1/81 : 1/81)

Each edge of a square, defined by N_1P_1, N_1P_5, N_5P_5, and N_5P_1, as the corners, would represent a series of increasing concentration of one nutrient (limiting series), all other nutrients being present at constant level. A diagonal would represent a simultaneous increase in both nutrients (balanced series). The numerals in parenthesis (shewn above) represent the relative proportions of the nutrients in terms of the standard amounts given.

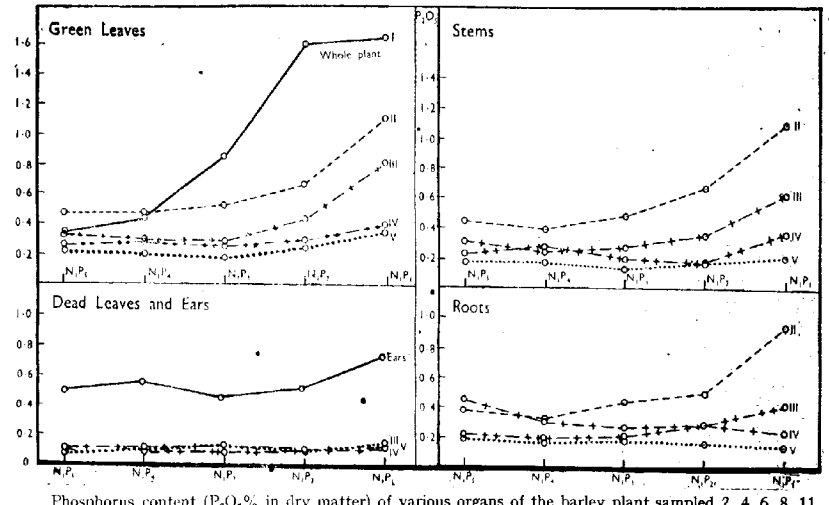
FIG. 1 A.



Phosphorus content (P_2O_5% in dry matter) of various organs of the barley plant sampled at 2, 4, 6, 8, 11 weeks (I—V) from germination.

$N_5 \rightarrow N_1$ increasing N supply (5 → 405 mg. N per plant).
P_1 maximum P throughout (135 mg. P_2O_5 per plant).
Nitrogen in minimum, phosphorus in excess.

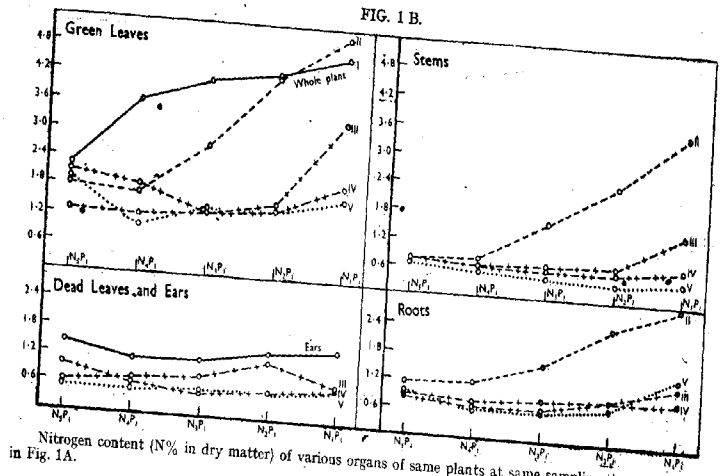
FIG. 2 A.



Phosphorus content (P_2O_5% in dry matter) of various organs of the barley plant sampled 2, 4, 6, 8, 11 weeks (I—V) from germination.

N_1 maximum N throughout (405 mg. N per plant).
$P_5 \rightarrow P_1$ increasing P supply (1.7 → 135 mg. P_2O_5 per plant).
Nitrogen in excess, phosphorus in minimum.

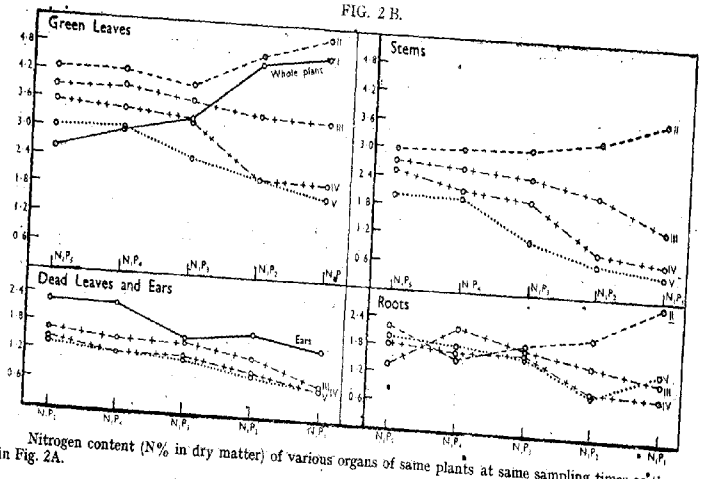
FIG. 1 B.



Nitrogen content (N% in dry matter) of various organs of same plants at same sampling times as those in Fig. 1A.

$N_5 \rightarrow N_1$ increasing N supply (5 → 405 mg. N per plant).
P_1 maximum P throughout (135 mg. P_2O_5 per plant).
Nitrogen in minimum, phosphorus in excess.

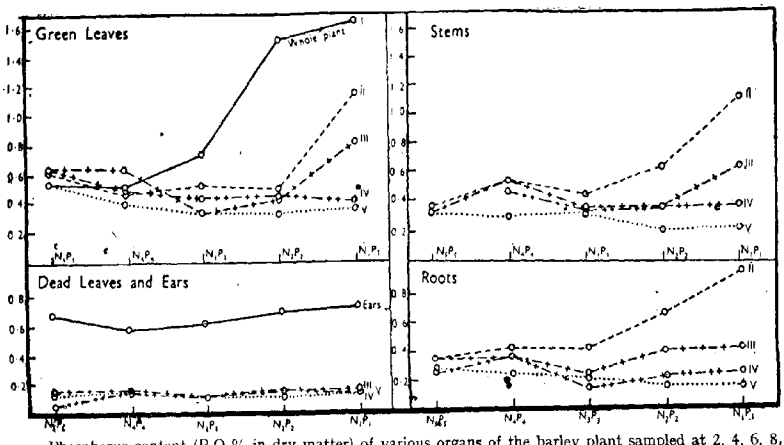
FIG. 2 B.



Nitrogen content (N% in dry matter) of various organs of same plants at same sampling times as those in Fig. 2A.

N_1 maximum N throughout (405 mg. N per plant).
$P_5 \rightarrow P_1$ increasing P supply (1.7 → 135 mg. P_2O_5 per plant).
Nitrogen in excess, phosphorus in minimum.

FIG. 3 A.



Phosphorus content (P_2O_5% in dry matter) of various organs of the barley plant sampled at 2, 4, 6, 8, 11 weeks (I—V) from germination.

$N_5 \rightarrow N_1$ increasing N supply (5 → 405 mg. N per plant).
$P_5 \rightarrow P_1$ increasing P supply (1.7 → 135 mg. P_2O_5 per plant).
Nitrogen and phosphorus balanced.

The variation in yield obtained in this series of cultures is shewn in Table III. The yields are given in gm. dry matter of grain per pot of 3 plants, and expressed on an acre basis would correspond to an extreme range of 1.0 — 47.5 cwt.

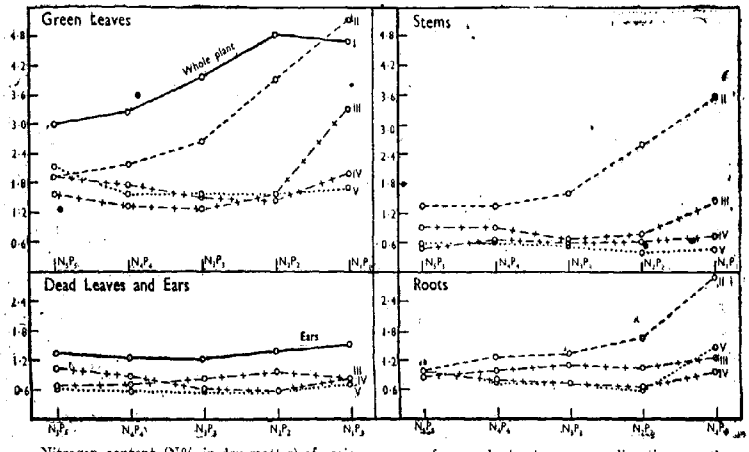
Table III

Yields of barley plants under varying nitrogen and phosphorus nutrition (gm. per pot of grain, dried at 100°C.)

	P_1	P_2	P_3	P_4	P_5
N_1	33.0	18.9	2.70	1.32	0.70
N_2	10.54	10.86	4.94	3.59	2.45
N_3	4.64	4.43	4.20	3.50	3.47
N_4	1.98	1.94	2.20	1.97	1.27
N_5	1.20	1.22	1.04	1.20	1.00

The internal concentration of nutrients for the series with phosphorus at high level and increasing doses of nitrogen are given in Fig. 1, those with nitrogen at high level and increasing doses of phosphorus are shewn in Fig. 2, while the data in Fig. 3 refer to the "balanced" series.

FIG. 3 B.



Nitrogen content (N% in dry matter) of various organs of same plants at same sampling times as those in Fig. 3A.

$N_5 \rightarrow N_1$ increasing N supply (5 → 405 mg. N per plant).
$P_5 \rightarrow P_1$ increasing P supply (1.7 → 135 mg. P_2O_5 per plant).
Nitrogen and phosphorus balanced.

For each of these series, two diagrams are given, A representing the percentage of P_2O_5 in the tissues and B the percentage of nitrogen. It should be emphasized that the analyses in Figs. A and B relate to the same set of plants, so that the relative internal concentrations of nitrogen and phosphorus for each manurial combination can be ascertained. Furthermore, the concentrations in various organs of the plant are presented, namely green leaves, dead leaves, stems, roots and ears. The plants were sampled on five occasions during growth, viz. 2, 4, 6, 8 and 11 weeks from germination. The curves referring to these sampling occasions are numbered in Roman numerals (I—V). On the first sampling occasion the organs were not separated, and the curves for the whole plant at this time are entered with those for the green leaves, which at this time formed the bulk of the material. The data for the ears are entered with those for the dead leaves; for the latter only three curves are given, since before the sixth week very few dead leaves were present.

The rate of uptake of the nutrients immediately after germination will depend upon the concentration of the nutrient at the root surface. In consequence of the uptake, growth will proceed, and, if the nutrient is primary and determines meristematic activity, as in the case of nitrogen or phosphorus, the rate of laying down of new meristems and differentiation of primary meristems will be determined by the internal concentration. But it must be realized that the position of the new meristems is determined by the structure of the plant. Thus, in the cereal a new branch (tiller) is laid down in the axil of every early leaf; as development goes on new possible positions of branches appear, and the whole system tends to extend exponentially. The rate of development is, however, circumscribed and controlled by the external factors of light, temperature, water and so on. If these are present at optimal level, development will reach its maximum possible value. Not only does the shoot of the plant develop in this way, but the root system also, and as the total uptake depends on the extent of the root surface the uptake will also tend to increase exponentially (with increasing velocity). The concentration of the

nutrient in the soil solution is the other factor concerned in total uptake,* and as this tends to be high in spring uptake in the early stages of growth will be high for this reason and tend to fall as the nutrients are exhausted. Other factors, themselves determined by the balance of nutrients, are concerned—namely the relations of growth of root and shoot, which complicate the issue but do not fundamentally change the picture.

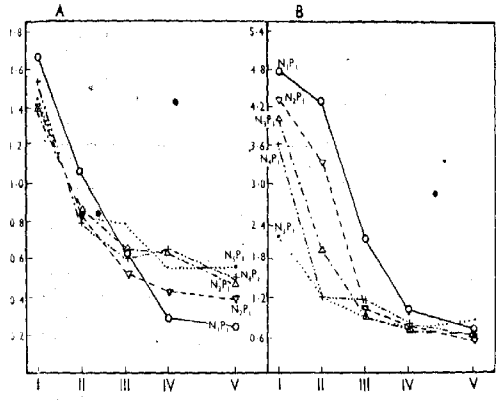
In the early stages of growth, then, concentration of the nutrients will be high since the supply is high and demands are then low owing to the few growing points present at that time. In the interaction experiment already described, high concentration at first was secured by addition of the total nutrient dose before germination. The variation of the external concentration is reflected in the whole plant analyses, sample I. In Fig. 1B, nitrogen concentration rises with increasing nitrogen supply, and in Fig. 2A a similar result is seen for phosphorus where phosphorus doses increase. Comparing Figs. 1A and 1B, it is seen that, so far as phosphorus content is concerned, where phosphorus level is the same throughout the series the internal concentration in the plants remains high and nearly constant. In Fig. 2B, as contrasted with Fig. 2A, the internal nitrogen concentration, although at a constant level of supply, shews a rise as the phosphorus level is increased. This may perhaps be accounted for by the fact that the nitrogen content of the roots is always lower than that of the green portions, and with low external concentration of phosphorus the roots form a relatively high proportion of the plant. Since sample I consists of the whole plant, the proportion represented by roots decreases as the level of phosphorus is raised, and hence the percentage content of nitrogen tends to rise. In the case of phosphorus, the percentage content of the roots is similar to that in the aerial portions, and consequently the concentration of phosphorus in the whole plant (Fig. 1A) is uniform throughout the series. By the time of the second sample this effect is no longer apparent, and in Fig. 2B all organs of the plant at this stage display only small differences in nitrogen content with increasing phosphorus supply.

The changes in concentration in the various organs during the growth cycle are clearly shewn in all the diagrams. In leaves, stems and roots the concentration of the nutrient in minimum falls, so that by harvest the internal concentration of the nutrient in minimum is always low and almost independent of the original external supply. This can be seen for nitrogen in Fig. 1B and for phosphorus in Fig. 2A. It should be noted that this low content independent of supply is seen in the dead leaves as early as the third sample, which is a consequence of the mobilization of the nutrient from the senescent leaves to supply the meristems. The changes in internal concentration during development are the greater, the higher the original level of supply of the nutrient "limiting" growth—best seen in the stem data in Fig. 1B, and those for leaves and stems in Fig. 2A. The relation of external supply to internal concentration of the other nutrient, always at high level, is in marked contrast, as seen in Figs. 1A and 2B, in the following respects. At the time of the second sample, in all organs the internal concentration is almost unaffected by the supply of the other nutrient, and as sampling progresses the internal concentration of the nutrient at high level falls more and more, the greater the supply of the "limiting" nutrient. This is well shewn in all organs of the plant, and is a result of the greater growth made with increasing supply of the nutrient in minimum. In consequence, at harvest the concentration of the element in relatively high supply remains high. The same relations are seen in the dead leaves, indicating that the nutrient in abundant supply is not mobilized from the senescent portions. This is the principal meaning of "luxury consumption." Where the nutrients have been supplied in balanced proportions, these effects of "luxury consumption" are not seen. Figs. 3A and 3B shew that the behaviour with regard to internal concentration of both nitrogen and phosphorus is very similar, and resembles that already found for the nutrient "limiting" growth in the other two diagrams.

The combined effects of the changing concentrations in the organs during development are shewn in Figs. 4—6, where the internal concentrations in the whole plant of nitrogen and phosphorus are presented at the various sampling occasions. As in the separate organs, the concentration of the nutrient in minimum displays large differences in the earlier samples, but the curves converge to a low level by harvest (see Fig. 4B for nitrogen and Fig. 5A for phosphorus).

* Actually the nutrient concentration within the conducting tissues of the root is also involved, since the rate of uptake depends upon the concentration gradient across the outer tissues of the root.

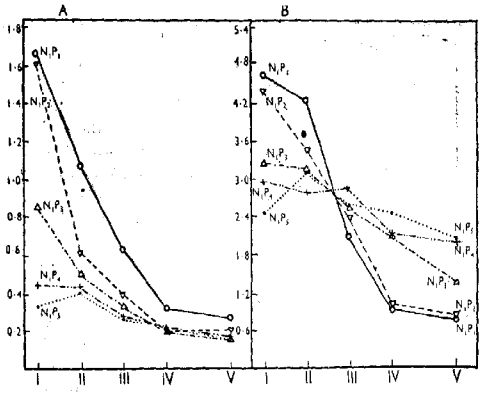
FIG. 4.



Drift of phosphorus (A) and nitrogen (B) (% content in dry matter) in whole barley plants sampled 2, 4, 6, 8, 11 weeks (I → V) from germination.

Nitrogen varying and phosphorus maximal.

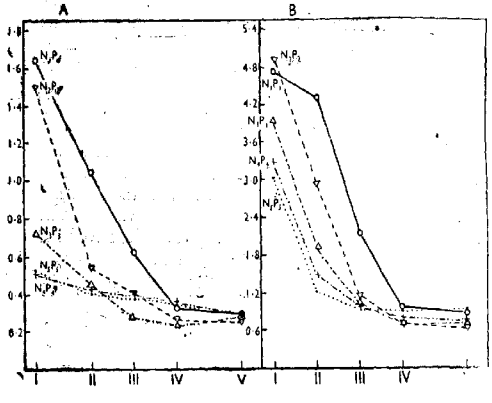
FIG. 5.



Drift of phosphorus (A) and nitrogen (B) (% content in dry matter) in whole barley plants sampled 2, 4, 6, 8, 11 weeks (I → V) from germination.

Nitrogen maximal and phosphorus varying.

FIG. 6.



Drift of phosphorus (A) and nitrogen (B) (% content in dry matter) in whole barley plants sampled 2, 4, 6, 8, 11 weeks (I → V) from germination.

Nitrogen and phosphorus varying together; balance of N : P_2O_5 constant at 3 : 1.

The relations for the nutrient in constant high supply are seen in Figs. 4A and 5B. In the former case the concentration of phosphorus varies little at the first sample, but large differences appear by harvest, at which time the series of increasing nitrogen supply appears as a series of falling internal phosphorus concentration. The same kind of relation, though much more marked, is seen for nitrogen in Fig. 5B, which represents the nitrogen concentration in plants with high constant nitrogen supply and increasing phosphorus. The order of nitrogen concentration undergoes a complete reversal between the first sample and harvest, and the curves intersect at a single point (some five weeks from germination) *at which time plants of very different size have uniform nitrogen concentration.* The curves in Fig. 6 refer to the " balanced " series, and these both resemble each other in general type and are similar to the corresponding curves for the element in minimum—thus, Fig. 6A resembles Fig. 5A, and Fig. 6B Fig. 4B. A similar kind of relation has also been shewn to hold for the interaction of nitrogen and potassium (Gregory, 1937, and Fig. 2).

The elucidation of the results just presented would require a lengthy discussion of the mode of growth and changes in growth rate of different organs throughout development in the different series. Some data bearing on these relations have been presented elsewhere (Gregory, 1937). Suffice it now to say that the continued development of each meristem is exponential, while at the same time new growing points develop, so that an ever-increasing demand is imposed upon supply for further growth ; eventually demand overtakes supply, and a condition of "internal starvation " supervenes. This is reflected in the increasing senescence of the organs first formed, and in mobilization and transfer of some nutrients thence to the parts still meristematic. The nutrients differ in this respect, for whereas, as has been indicated above, nitrogen, phosphorus and potassium readily become again available, this is untrue of calcium. Among the minor elements, boron is mobilized only to a slight extent (Cooper, 1937 ; Wolf, 1940).

These considerations bear on the problem under discussion in two ways : (1) the concentration in the tissues will depend upon the time during development at which determinations are made ; (2) the results will depend upon the part of the plant chosen. Analysis of the plant soon after germination (as soon as seed reserves are exhausted) will give some measure of the concentration of the nutrients in the rooting medium. The data for barley already dealt with shew this clearly, and with cotton Crowther (1941) has shewn that by analysis of the leaves within the first two months after germination the yield could be forecast with a high order of accuracy. It should not be supposed that the nutrient concentration at this stage of development will in all cases represent the maximum correlation with yield ; other types of plant which do not branch very rapidly in the early stages may not display the phenomenon of " internal starvation," which has been postulated for the cereal type of development—on which this high correlation with yield ultimately depends.

The rather lengthy discussion refers to plants grown under somewhat artificial conditions, and it is necessary to consider the bearing of the ascertained facts on the relations to be expected with plants growing in the field. The outstanding difference arises from the mode of supply of the nutrient, for, first, although in the field the concentration in the soil solution tends to be higher at germination than later in the season, the differences in concentration encountered are of quite a different order from those employed in the sand cultures described. Second, the nutrient supply to the soil solution is a continuous process, and the rates at which the nutrients become available are likely to be more important than the actual concentrations—indeed, under a crop the concentration in the soil solution may fall almost to zero, owing to the more rapid uptake by the plant than the rate of release from the soil particles. Third, in certain types of plant with large capacity for meristematic multiplication, such as barley, it is found that at a certain stage (in this case, flower differentiation) further elaboration of meristems ceases, and therefore nutrients taken up after this stage lead to no further increase in yield, but instead the nutrient absorbed raises the concentration within the plant and checks the normal tendency to decline to a minimum at harvest irrespective of the original supply level. It is therefore not surprising to find that plant analyses from field crops can display considerable variations in concentration at the stage of harvest. In dealing with the literature many examples have been cited of high concentrations of nutrient in the mature cereal plant ; this may be due to two different causes : first, the limitation of growth by some other nutrient factor leading to "luxury

consumption " ; second, a high supplying power of the soil maintained throughout the growing period. In the former case yield will tend to be low and could be improved by the addition of the nutrient in minimum ; in the latter case, yield will be high. The proposals to use analyses of mature cereal plants as indicators of the nutritional status of the soils on which they were grown thus depend upon the fact that differences in the nutrient-supplying power of the soil persist throughout the growing season, leading to accumulation in the later stages, and not upon any direct causal relationship between final internal nutrient concentration and yield. The utility of top dressings for increasing yield is entirely limited by these facts, for if supplied after the critical phase is past the nutrient supplied may have no effect on yield.

RELATION OF YIELD TO INTERNAL NUTRIENT CONCENTRATION

The preceding discussion has dealt with the effects of varying nutrient supply on yield and on nutrient concentration within the plant. It is now necessary to pose the question of the relationship between the latter two quantities. It has been shewn that as the level of a nutrient not in ample supply is increased, other factors being held constant, both yield and internal nutrient concentration rise—at least in certain plant organs and at certain stages of development. Indeed, attempts have been made to express this relationship in a mathematical form ; Pfeiffer *et al.* (1919) proposed a hyperbolic formula, Gast (1937) found the yield of pine seedlings to be linearly related to the logarithm of the internal nitrogen concentration, while Mitchell (1939) found the relation between yield and internal nutrient concentration to be nearly linear until the maximum yield was reached. Macy (1936) distinguished three portions of the curve relating yield to internal concentration—the " minimum percentage" portion where yield rises, although internal concentration remains constant (presupposing a minimal concentration in the plant, c.f. Heinrich, 1882 ; von Dikow, 1891 ; Helmkampf, 1892) ; the " poverty adjustment" region, in which both yield and internal concentration increase ; and finally a " luxury consumption " region in which yield remains constant with rising internal concentration. The transition from the " poverty adjustment " to the " luxury consumption " region took place at the " critical percentage." These interpretations apply to a situation in which one nutrient only is varied, and presuppose that yield rises with increasing supply of this nutrient—i.e., that growth is "limited" by this nutrient. If however the conditions studied cover a wide range of combinations of nutrient factors, it is clear that the internal concentration of one alone of these nutrients is unlikely to be related to yield over the whole range. Such varying combinations are in fact found in the field, as is shewn by the varying manurial responses of plants in different soils.

A method for the diagnosis of fertilizer requirements is not directed primarily to forecasting the yield, but rather to forecasting the response of the plant to the addition of a nutritive element, so that by providing this after diagnosis yield may be improved. The minimal requirements to develop such a method would be data for plants growing in a series of substrates at various levels of one factor with the others in excess, including first the internal concentration of the varying nutrient at a definite stage in definite organs; and second the increase in yield resulting from the application of a definite quantity of the nutrient at this time. The increments in yield resulting from this specified addition of nutrient could then be represented graphically as a function of the nutrient concentration within the plant at the time of application. Such a graph would form the basis for forecasting the effect of the nutrient addition. Data of this kind have been presented by Crowther (1937), Craig (1940), Lundegårdh (1941) and Emmert (1942a). Lundegårdh claims that for a single nutrient the relationship can be expressed mathematically by an equation of the type

$$y = \frac{a}{x^c}$$

where y is the yield increment resulting from the addition of a specified amount of nutrient and x the concentration of this nutrient in the plant at flowering time, a and c being constants.

It is important, however, to consider the effect of the levels of other factors on the postulated relationship. It has been claimed by Pfeiffer *et al.* (1919) that this relationship, when expressed in terms of percentage increment in yield is independent of the supply of other nutrients and of environmental factors ; but relative yield increments are of no practical importance since the

absolute increase is not implied. Macy (1936) claimed that his "critical percentages" were largely independent of the level of the other "ordinary growth factors," while Chapman (1941) considered that in his data for rubber the relationship between growth and internal nutrient concentrations followed a law of limiting factors*—which would be in line with the suggestion frequently made (Wallace, 1928a; Thornton, 1932; McDonald, 1934; Thornton *et al.*, 1934; Scarseth, 1941, 1941a; Ulrich, 1944) that plant analysis will often shew only which nutrient is "limiting." It may be doubted, however, whether these claims could be maintained as generalisations in face of the evidence provided by Lundegårdh (1941) that the absolute increment in yield resulting from a given fertilizer application to plants with a particular internal concentration of the nutrient supplied in it is markedly affected by the level of other nutrients (Table VI); see also Emmert, 1942a). The yield increment as determined by more than one factor was considered by Lundegårdh to be represented by a general equation of the form

$$y = \frac{k}{x_1^{c_1} \cdot x_2^{c_2} \cdot x_3^{c_3}}$$

so that for many factors acting simultaneously the yield increment is proportional to the product of the effects of the single factors. The question as to whether this equation correctly represents the relationships is not a matter of immediate concern, and the evidence in support of it is far from conclusive.

In the method outlined above, the effect of the other factors on yield increment can be ascertained by analysing the plants for all the nutrient factors at the time of application. In this way, the yield increment can be represented in terms of combinations of concentrations, which for two factors could be portrayed in a solid diagram. For more than two factors the relationships could be represented algebraically by regression equations. At present no adequate data of this kind are available, though Lundegårdh's work indicates the direction in which progress can be made.

In spite of the view of Pfeiffer and his colleagues already quoted, it would be unwise to rule out the possibility that the relation between plant composition and increases in yield due to nutrient supply may be affected by differences in external factors such as light, temperature and water supply. Mitchell (1934), for instance, published results suggesting that light intensity affected these relationships in pine seedlings; work at Lichterfelde (Eckstein *et al.*, 1931) indicated that shading affected potassium relations in potatoes; and Nightingale (1942) found that the nitrate content in the pineapple corresponding to optimal nitrogen nutrition was higher when conditions favourable to assimilation led to a high starch content than when it was low.

POSSIBLE DIFFICULTIES IN THE DIAGNOSTIC USE OF PLANT ANALYSIS

Before considering practical aspects of the proposals for the diagnostic use of plant analysis, it will be helpful to indicate conditions, which might be encountered in practice, under which such diagnostic methods must fail. The validity of the use of plant composition as a diagnostic index depends upon the assumption that to each set of concentration data there corresponds a unique potential response in yield to the application of each nutrient at that time or subsequently. If the same plant composition is associated with more than one potential yield response to fertilizer application, it is self-evident that analysis of the plant can provide no means of distinguishing between these diverse possibilities. That this does in fact hold, at least over certain ranges, has several times been suggested. The view has been ascribed to von Liebig, as a corollary to his "Law of the Minimum," that the composition of any plant species is constant (Thomas 1929, 1934), though in fact von Liebig (1863) seems to have limited himself to postulating that the proportion of the various ash constituents to one another is constant—and in some species at least he admitted the possibility of mutual replacement of bases (1840, 1863); Joulie (1876) has

* c.f. also the remark of Heinrich (1882), in regard to the composition of oat roots, "that that component which is present in smallest quantity decides the yield and determines whether the crop shall be light or moderate. The other nutrients may then be present in much greater amounts . . . . without causing any increase in the yield."

also been quoted (Lagatu and Maume, 1927) as considering that each species had a typical composition, from which only slight deviations occurred; but he continued by shewing how potassium deficiency in wheat could be diagnosed by the difference in composition of good and bad plants from the same field. In spite of the many tabular presentations of "typical" composition of plant organs, it is doubtful whether the view has ever been seriously held that the composition of any plant or organ is invariable.

A variant of this view ascribed to von Liebig lies in the possibility of minimal nutrient concentrations within the plant—that is, it has been suggested that if the supply of a nutrient is progressively reduced, the percentage of that nutrient in the plant diminishes only to a certain point, and then remains constant, although yield continues to decrease. As shewn in the previous section and in Table XII, several of the earlier workers attempted to determine such minima; whether this is in general a correct representation of the course of change of nutrient content with nutrient supply is, however, doubtful,—although, as has been shewn for cereals (Figs. 1—3), as growth proceeds the internal concentration tends to a constant minimal value irrespective of original supply. Under such conditions, it would follow that it would be impossible to distinguish by plant analysis between different levels of deficiency falling within this minimum zone. If a maximum nutrient content were reached at a nutrient supply level insufficient to give maximum yield, this would likewise reduce the value of plant analysis for diagnostic purposes; von Dikow (1891) and Helmkampf (1892) postulated such a maximal nutrient content, but seem to have envisaged it as being reached only at a nutrient supply level such that further additions cause no further increase in yield; a maximum of this type would be no disadvantage to the diagnostic use of plant analysis. Süchting (1939) found that in forest tree seedlings supplying a nutrient to plants severely deficient in it caused increases in both yield and the nutrient concentration within the plant, but that at less severe levels of deficiency increases in nutrient supply caused further increase in yield without any accompanying increase in internal concentration. It should be noted that this result carries a rather surprising implication—that, with increasing nutrient supply, raising the percentage nutrient content within the plant takes precedence over utilization of the increased uptake for further growth; it is clear, however, that in any case where such relationships obtain diagnostic plant analysis would be useless over the range where nutrient content is at its maximum level.

Another possible type of relation between nutrient supply and internal nutrient concentration, which would to some extent invalidate the diagnostic use of plant analysis, would include all those in which the same nutrient content might be situated on both an ascending and a descending limb of the curve—that is, where with increasing nutrient supply the internal nutrient concentration reaches and passes a maximum or minimum value. That this may sometimes happen is suggested by the work of Piper (1942) on copper deficiency in oats, and by some of the early work on the nitrogen content of cereals. Piper suggests, however, that the rather higher copper content of plants grown with the lowest copper supply level than that of those receiving a little more was due to the immaturity of the former when harvested, and that, if both had been harvested at a comparable stage of development, the copper supply would have been reflected faithfully in the copper content of the plant material.

In relation to the numerous proposals for using plant analysis to determine the fertilizer requirements of soils for future crops, a further possible way in which the technique might break down can be envisaged. In cereals, for instance, as already stated, after ear formation is well advanced further additions of nitrogen-containing materials cause no increase in yield, although they increase the percentage of nitrogen in the plant. Thus a given final nitrogen content may be the result of a nitrogen supply that increased sharply during a late period of development from a previously low level, or may be the result of a moderate level of nitrogen supply throughout development. In the latter case, the yield will be higher and the yield response to added nitrogen lower than in the former case. In fact, were such differences in the course of seasonal changes in nitrogen supply to occur, the usual relationship might even be reversed, and the higher final nitrogen content be found in those plants that would have responded more markedly to extra nitrogen supply at the beginning of growth. Since, however, cereal soils shew very marked and consistent decline in nitrogen supply level during the growing season, this is unlikely to be a source of difficulty in practice.

Certain other circumstances have from time to time been adduced as diminishing the possible value of plant analysis as a diagnostic procedure. The first of these is the existence of " luxury consumption " ; it has been argued that the fact that a plant may continue to accumulate a nutrient to a level far above that giving the maximum favourable effect on yield prevents the observation of an increase in nutrient content being any indication that this increase has been accompanied by or responsible for an increase in yield. As far as it goes, this statement is of course true ; but to argue from this that " luxury consumption " might interfere with or invalidate the diagnostic use of plant analysis, as has been done by Hanamann (1904), Nolte (1927) and Hardy (1937), is unjustified ; its existence certainly prevents the relation between yield and internal concentration of nutrient being linear over the whole range, but so long as adequate standards for the relationship between nutrient percentage and increase in yield as a result of treatment have been set up, " luxury consumption " is irrelevant to nutritional diagnosis.

It has also been argued (Hall, 1905 ; Münter, 1919, 1920, 1920a) that the fact that plant composition is greatly affected by seasonal variations in weather—often more than by manurial treatments—reduces very greatly its value for diagnostic purposes. This may be true if it is required to provide indications of permanent soil characteristics ; but, if plant analysis is regarded as providing an index of the state of the plant analysed rather than of the soil, this fact need in no way be a disadvantage—rather the reverse. Such differences in composition are often associated with real differences in the potential responses of the plants to manurial treatments, and so long as the relationship between such potential responses and plant composition remains unaffected by seasonal variations in weather the value of plant analysis for diagnostic purposes is in no way diminished by such observations.

SELECTION OF A TECHNIQUE

The investigator entering for the first time upon the use of plant analysis for the diagnosis of the nutritional status of a particular crop plant has a very wide choice of possible alternative techniques to adopt—the various times during the season at which samples may best be taken; whether the whole plant should be gathered or some particular organ; whether the analysis should be conducted on the whole plant material or an extract of it; for the whole of the element in question or some particular chemical fraction; and finally how best the analytical results when obtained may be interpreted—all these are questions on which decisions have to be made, and here, as has been shewn, theoretical considerations give little guidance.

Many investigators have tacitly ignored these questions; a certain technique has been arbitrarily selected and, since it has yielded results, has been continued without regard to the possible improvements which might result from modifications. These investigators have often been satisfied if their method suffices to shew an increase in the content of a nutrient following the application of an appropriate fertilizer—quite apart from the effects of such treatments on yield, or of the relative importance of the different nutrients in the fertilizer mixture. Such a criterion may be valid if the nutrient supply from the soil is the principal subject of interest, but has obvious shortcomings if the method is intended to determine quantitatively fertilizer requirements. As already indicated, the correct criterion for assessing the value of any method purporting to be applicable to the determination of fertilizer requirements is the agreement between forecast and actual yield responses to fertilizer treatment. If the adoption of a technique, however arbitrary, can be supported by evidence of this kind, the question arises whether it is worth while to attempt its improvement. It needs to be pointed out that the labour and time required to make a satisfactory comparison between different possible techniques is very considerable. Consequently, if standard values (see pp. 92-106) have already been ascertained, an attempt to improve the method may well be unjustified, unless a comprehensive investigation over a number of years is in view. On the other hand, if the standard values have not yet been determined, little additional effort may be required to include more than one possible technique in the experiments to determine such standard values, and subsequently only that technique need be employed which has given the most satisfactory results in the preliminary work. A further point to be remembered, when considering to what extent the effort necessary to improve a technique is remunerative, is that the best technique for the determination of fertilizer requirements is likely to differ as between different nutrient elements and may even vary with the amount of the fertilizer application the effect of which is to be predicted; in practice a compromise may become necessary.

Of those workers who have not arbitrarily selected a diagnostic method, some have attempted to decide on *a priori* considerations in favour of one or another technique, but the arguments put forward can usually be confronted by others supporting another conclusion; for instance, it has been urged that the older leaves should be selected for sampling, since under conditions of nutrient deficiency a considerable proportion of their nutrient content is translocated to the growing regions, while on the other hand that meristematic regions should be analysed since it is there that differences in nutrient content exercise a direct influence on growth. Other workers have proceeded on the assumption that those sampling and analytical techniques giving the greatest differences (absolute or relative) between plants differing in nutrient status will be the most satisfactory; this criterion will be discussed at greater length later. Still other investigators have attempted to use criteria such as the correlation of the analytical data with results of soil analysis by some accepted method, or with the total nutrient content of the plant as a whole; it is clear, however, that in relation to fertilizer needs such criteria can only be of indirect value, depending upon the correlation of soil analysis or the nutrient content of the whole plant with fertilizer needs. Some workers have judged the value of a method for nutritional diagnosis

on the basis of the relation of the concentration of a nutrient in the plants to growth or yield ; this is justifiable where one can be satisfied that differences in the uptake of one nutrient only are responsible for the differences in behaviour of the plants—otherwise, as shewn on p. 57, the relationship cannot be expected to persist.

In view of the considerations put forward it is clear that the value of any method for determining fertilizer requirements from data of plant analyses depends upon the accuracy with which the response to fertilizer additions can be forecast. That is, the primary need is knowledge of the relation between the actual observed yield increment resulting from the treatment and predicted values based upon plant composition.

It is evident that a prerequisite for the application of this criterion is a series of comprehensive experiments in which plant material samples have been taken for analysis *before* the fertilizers, whose effects are to be predicted, have been applied. If the purpose of the diagnosis is to find the fertilizer requirements for crops subsequently grown on the same soil, this involves the determination of yield responses for a crop following that from which the analytical samples have been taken. In fact, few such data are available (for examples, see Wagner, 1915), and have never been used for the purpose indicated. It is true that data have frequently been presented on the composition and yield responses of plants which had received various fertilizer treatments at the beginning of growth, but the relevance of such data depends on the correlation of the yield response of one crop with that of another crop grown subsequently on the same soil—and such correlations are far from perfect.

In the comparison of various possible techniques, however, the varying conditions from year to year are likely to affect conclusions as to the relative value of different techniques to a much smaller extent than the actual level of standard values determined, and hence data of the type described can probably be applied much more usefully for such comparative purposes than for obtaining standard values relating plant composition to prospective yield increase following applications of fertilizer. The advantages of artificial culture methods, either in sand or solutions, indicate their use for comparing techniques, though their dissimilarity from conditions in the field will restrict their use for determining standard values. It hardly needs stressing that the data collected for selecting a diagnostic technique, whether in artificial culture or in the field, should, if possible, cover the whole range of conditions to which it is intended the technique should subsequently be applicable.

Most investigators are not in a position to set up special trials with a wide variety of conditions in which responses can be observed and samples for analysis collected according to the various techniques which it is proposed to test. Most often they are obliged to rely upon samples taken from fertilizer trials already established with other purposes in view. They may be able, in such a case, to treat the varying conditions, other than the supply of the nutrient under consideration, as providing separate units of data from which correlations of the type indicated above may be computed. The more usual procedure is to compare the composition of those plants receiving and not receiving the nutrient in question, and it is argued that the method whose results shew the most marked difference between these two groups of plants is to be preferred. But this argument may be fallacious, if either the standard error or the coefficient of variability of the analytical results obtained on replicate samples under the different methods are different, which may often be the case. Data of Pfeiffer *et al.* (1912), for instance, shew that in oats with intermittent water supply, though the proportional increase in the nitrogen content of oat straw with added nitrogen is considerably greater than that in the grain, the coefficients of variability for the former figures are so much higher as to make the grain composition a more trustworthy index of response. Nevertheless, when no other criterion is available, this test of the proportional increase in nutrient content may be of some value—where, for instance, a perennial crop is concerned for which the establishment of *ad hoc* fertilizer trials on a large scale is impracticable—especially if the method of analysis employed involves a large and fairly constant coefficient of variability, as is the case with many colorimetric and spectrographic methods.

A modification of this approach which would have rather better justification but which, so far as the authors are aware, has never been used, would be to compare, instead of the differences between treated and untreated plants, the ratios of these differences to their standard errors (t values).

Where yield response and nutrient content data are available the techniques of correlation and regression can usually be fruitfully applied. A warning needs to be given, however, against the uncritical acceptance of results by the standard correlation technique. This technique is devised for estimating the relationship of two quantities *linearly* dependent upon one another—and we have seen that there is no reason to suppose that the relationship between yield response and nutrient content is linear. Accordingly, account should be taken of the possibility that the relationship is curvilinear; since no assumption can be made on the form of the curve, it is probably best to try to fit a polynomial expression :—

$$y = a + bx + cx^2 + \ldots .$$

where y is the yield response, x the nutrient content, and the remaining terms constants. Where data on simultaneous variation in more than one nutrient are available, the values may be analysed by the method of multiple regression—the possibility being again borne in mind that the relationships with the different nutrients may shew independent curvature.

It is necessary at this point to refer to the arguments brought by Thomas and Mack (1944a) against the use of statistical methods in interpreting the results of analytical diagnosis. They argue that " the use of calculations of probability in such a manner as to submerge or include specific and particular properties of individuals, such as leaf composition, into an abstract quantity is opposed to the whole spirit of biology and is logically not permissible". They appear to regard as inacceptable the lumping of data from similarly treated plots, whether of yields or of chemical composition. They do not appear to realize, however, that this consideration applies with equal force to individual plants within a plot as to replicate plots; they sample for analysis only those plants which appear typical of the plot, and yet their yield data presumably derive from all the plants on the plot. It may be admitted that for the purpose in view the random variation of yields from replicate plots about their mean value may provide further data for ascertaining the relation between plant composition and prospective yield, since it may be anticipated that these variations in yield may be highly correlated with plant composition, and, if so, this relation can be determined from such data for replicated plots, though perhaps not so accurately as from individual plants. Where data are available for individual plots or plants of both plant composition and yield, use would naturally be made of all such individual groups of data for assessing the relation sought, and not of treatment means only. This does not circumvent the use of the appropriate statistical methods for determining the magnitude and significance of the relation, for without such tests it is impossible to determine whether the observed differences in yield and chemical composition are consistently related.

The error of a technique of analytical diagnosis may be conveniently divided into three portions :—that of the analytical procedure, that of the sampling method, and that of the standard values.

With standard chemical methods the analytical errors will generally be negligible compared with the errors from other sources (if the analytical error is one-fifth as great as the total error, its complete removal will only reduce the latter by some 2%), but with some of the rapid methods in current use it may make an important contribution to the total error.

The errors of sampling need no further comment. By including in the sample for analysis material from an appropriate number of plants distributed over the area under study, they can be brought to a satisfactorily low level.

The errors of the standard values are much more complex, and include those involved in the determination of the relations between plant composition and yield response to fertilizer in the experimental data collected for this purpose, and those due to differences between the conditions prevailing during the growth of the standard plants and of plants in other investigations. The first group of errors will be systematic—that is, they will have similar effects on all diagnostic conclusions; the second group will also be systematic in so far as they may be ascribed to deviations of the conditions under which the standard values were obtained from the mean of the range to which it is intended they should be applicable. These systematic errors can be reduced by increasing the number and range of experiments on which the standard values are based. The remaining portions of this group of errors will probably be random, like those due to sampling and the analytical methods.

To summarise the preceding paragraphs: the only satisfactory basis for comparing the relative value of different possible techniques for analytical diagnosis is the deviation of the various estimates of increase in yield following a given fertilizer treatment from the actual increase observed when the same treatment has been applied subsequently to the time of sampling the plants for analysis. When this criterion cannot be applied, the yield responses to treatment applied prior to sampling (though at the proper time of year or stage of development) will provide fairly satisfactory data. If yield response data are not available, some idea of the relative value of different indices of nutrient status may be obtained from the absolute or relative differences (or, better, their ' t ' values) in these indices between plants under different conditions of nutrition.

SELECTION OF PLANTS FOR SAMPLING

Where the purpose of diagnostic plant analysis is the determination of the characteristics of the soil with a view to modifying the fertilizer regime for future crops, it may be necessary to determine what plant species provide the best indication of fertilizer requirements. Oats was selected by many of the early investigators, some giving as the reason that it was normally grown after the soil had been to some extent exhausted of phosphorus and potassium by previous crops in the rotation (Stahl-Schröder, 1904). In regard to copper deficiency in Australia, Teakle and his collaborators (Teakle, 1942; Teakle and Turton, 1943; Teakle, Thomas and Turton, 1941) found that oats, subterranean clover, vine, pear and apple were suitable plants to sample, though many other plants gave no reliable indication of the copper status of the soil. Robinson and Edgington (1942) found hickory leaves more suitable than those of other species for determining the boron status of soils, partly because they showed wide variations in composition, partly because they were little liable to soil contamination. But the selection of plants for analysis in such cases is often likely to depend upon which species are present rather than which are most suitable.

Where the problem is the correction of unsatisfactory nutritional conditions in the crop actually sampled, the selection of a suitable species does not, of course, arise. It is still necessary, however, to consider on what principle to select the individual plants—a decision also necessary where the nutrient status of the soil, rather than of the plant, is in question. If the yield response of a crop to fertilizer treatment were linearly related to the nutrient content in the material analysed, the matter would be relatively simple, for a random sample of the plants would give a correct indication of the response of the field as a whole. Where, however, luxury consumption occurs, this will not be true, for a random sample from a field in which some of the plants only are suffering from a nutrient deficiency will very probably contain enough material from plants in the luxury consumption range to push the mean nutrient content of the whole bulked sample into this range (Ulrich, 1943). Such observations have been made on apple, for instance, by Burrell *et al.* (1942), and this may well account for the irregular relationships between leaf scorch and potassium content of plum leaves found by Boynton *et al.* (1941). Some investigators, notably those of the " foliar diagnosis " school (see p. 41), recommend that samples should be taken from plants appearing typical of the area covered; Clements and Moriguchi 1942), in their work on sugar cane, sampled "*selected* plants representing the average of the stand"; Bathurst (1944a), too, in taking samples of citrus leaves, advises that they should be taken from trees " representative of the block as a whole". This procedure, of course, involves a subjective estimate of what is typical or representative, and therefore may, to some extent, be distrusted; moreover, it hardly covers the possibility of the area bearing a minority of plants with a deficiency among others with satisfactory nutrition.

It seems clear that, in order to obtain a clear idea of the range of nutritional conditions in the field or plantation, it will be necessary to take more than one sample, and to analyse each separately. Whether the separate samples are to be taken as representing different topographical divisions of the area (Yuen and Hance, 1939; Chem. Dept. Exp. Sta., H.S.P.A., 1944; Ulrich, 1944) or different types of growth of the plants (Bathurst, 1944a) is a matter that can hardly be decided without reference to the particular problem; where the latter procedure can be used on a tolerably objective basis, it is probably to be preferred. There seems, in any case, to be no reason to take replicate random samples covering the whole area.

TIME OF TAKING SAMPLES

Time of Day

Certain investigators have restricted the taking of samples for diagnostic analysis to a particular time of day. For rubber Chapman (1941) recommends that leaf samples should be taken between 6 a.m. and 10.30 a.m.; Mitchell and Chandler (1939) in their studies on forest trees preferred the mid-day period, 9 a.m. to 3 p.m. Nightingale's (1942) sampling of pineapple leaf bases took place between 8 a.m. and 4 p.m., while the Hawaiian Sugar Planters' Association (Chem. Dept. Exp. Sta., H.S.P.A., 1944) recommend that samples of sugar cane leaves should be taken during the first three hours after sunrise.

Few observations have been made on diurnal variation in the nutrient content of plant tissues. Schulze and Schütz (1909), Otto and Kooper (1910) and Pigorini (1914) found a decrease in the percentage nitrogen content in the dry matter of leaves overnight, while Kosutany (1897), Suzuki (1897) and Chibnall (1922) found increases in nitrogen content during the night. Ingalls and Shive (1931) found that the iron concentration in the sap of several species, especially succulents, increased during the day by as much as 40% of its mean value, and decreased again at night. McCool (1926) found the concentration of phosphate in the expressed sap of various plants higher during the morning than after mid-day. Penston (1935, 1938) found diurnal variations in the potassium content of potato leaves between 2.5 and 4.1%, and in maize leaves between 3.7 and 4.9%. Chapman (1941) stated that diurnal variation in mineral content occurred in rubber leaves. Bolas and Goodall (1937) found variations of up to 30% of the mean value in the ash content of tomato leaves during a 24-hour period, while Woodward *et al.* (1944) found the ash content of lucerne hay varied by as much as 40% of the mean with the time of day. Phillis and Mason (1942) found that the percentage content in cotton leaves of most of the mineral elements they studied decreased by day, but increased during the night. These results suggest that some control of the time of day at which samples are taken is desirable, but do not suggest any particular time as being preferable to others. Fonder (1929a) found variations of up to 25% in the calcium content of lucerne during the day; since variation was least marked between noon and 4 p.m., this period was recommended for sampling. Scarseth (1943), found that a plant suffering from inadequate nitrogen supply contained virtually no nitrate in the afternoon, though some was present in the early morning—indicating that later sampling may be preferable.

Time of Year or Stage of Development

Under this general heading also, the time of year at which samples are to be taken must be considered. For annual crops, when it is intended that the detection of unsatisfactory nutritional features shall be followed by corrective treatment of the same crop from which analytical samples were taken, the possible period over which samples can be taken is necessarily restricted to the period during which fertilizer treatments will be effective. In the choice of a sampling time it is necessary to take into account not only the accuracy of forecasting yield responses at different times, but also the actual extent of such potential responses at the same time. Consequently the tendency will be for sampling to take place as early as it can give definite indication of deficiency (Craig, 1939; Burkhart and Page, 1941).

Where the purpose of the sampling is to indicate treatments required by subsequent crops on the same soil, the criterion of correlation of analyses with yield responses will hold, except in so far as considerations of convenience enter. Although the proportional differences (or their errors) between analytical data for different fertilizer treatments have been used as evidence to decide the best stage for sampling, in annual crops at least it is a very doubtful criterion for this purpose, since these proportional differences are likely to be largely dependent upon seasonal changes in the availability of the fertilizer material. This objection does not, of course, apply to comparisons of plants grown on soils naturally well and poorly supplied with the element in question, and is less applicable to perennials, with their stored reserves of nutrients, than to annuals.

The problem of the best time for sampling is complicated by the seasonal variations in soil nutrient supply. As a result of these variations, the most appropriate stage of development may not be the same for widely different soil types or climates. The optimum time of sampling

may also be expected to differ for different nutrient elements, so that a single time cannot be optimal for all. Thus, in respect of time of sampling as well as many other points, it can only be hoped that the technique adopted falls within a fairly wide range around the optimum, and not that the absolutely optimal conditions can be found.

As indicated above (p. 56), theoretical considerations suggest that, in annual plants of the cereal type, analysis of samples taken early in the development of the plant may give the best indication of nutritional status. Crowther's (1941) observations on cotton grown on the same plot in successive years supports this, but his earlier (1937) comparisons of manurial trials shewed that the relative difference between nitrogen concentration in leaves from high nitrogen and low nitrogen plots increased to 140 days from germination, as also did the correlation of these nitrogen percentage data with yield responses at the various sites (omitting the aberrant result at Biba, $r = -0.343$ at 60 days, -0.660 at 140 days; $n = 8$). Nevertheless, a number of other observations support the use of early samples. Chapman (1935) found that the response of oats to phosphorus supply in pot culture (measured as total dry weight) was highly correlated with the inorganic phosphate content of different parts of the young plants, but that at the heading stage such correlations were much less marked and at ripening absent. Fraps *et al.* (1937) found the correlation of nutrient content of oats with soil supply better during early growth than as maturity approached. Salter and Ames (1928) found that the differences in nutrient content of maize plants with varying fertilizer treatment were greater at early stages of growth, and concluded that young plants might give better indications of soil productivity than older ones; since, however, the supply of all three principal fertilizer elements was varied simultaneously, this conclusion can only be accepted with reserve. Beath *et al.* (1939), in their investigations on selenium, found that differences in the percentages of this element in indicator plants were more marked at early stages of development. Forster (quoted by Teakle, Thomas and Turton, 1941) found that zinc deficiency in oats could only be detected by analysis if the samples were taken early in development, and Teakle, Thomas and Turton (1941) came to the same conclusion in regard to copper deficiency.

Burström (1937), in selecting a stage at which samples should be taken, proceeded on the assumption that under field conditions some variation in the sampling stage was inevitable, and that consequently a stage should be chosen at which such variation would have little effect on the analytical results (c.f. Stahl-Schröder, 1904—referred to on p. 15); this criterion was satisfied for oat leaves by the period between panicle emergence and flowering. Lundegårdh (1941) found that the relation of composition at this stage to growth was more constant than at an earlier stage.

It will be noted that, in the above paragraphs, the discussion has been mainly on the *stage of development* at which samples should be taken, and not of the *date*. If a date were to be specified instead, the relation between composition and yield response would be more likely to be affected by extraneous factors such as weather than if sampling occurred at a particular stage of development, irrespective of when this stage was reached.

For perennial crops, the purpose of analytical diagnosis is generally to remedy unsatisfactory conditions during the course of the following season, so that the choice of a sampling date need not be impeded by the need to obtain a result early enough to enable treatment to be carried out that same season. Some investigators have used the same criterion as that of Burström above; Mitchell (1936a), for instance, preferred the last two or three weeks before yellowing for sampling forest tree leaves, for this reason, while Boynton and his collaborators (Boynton *et al.*, 1940; Reuther and Boynton, 1940) found that the composition of apple leaves was most constant during late July and August. In California it was found (Chapman and Brown, 1943a; Chapman *et al.*, 1944) on this basis that July, August and September were the best months for sampling citrus leaves; on the other hand, Bathurst (1944a) preferred the winter (May-July in South Africa) for the same reason. Lilleland and Brown (1939) advised that plum leaves should be sampled before August, since at that time migration of potassium from leaves adequately supplied with that element commences; in peach, June and July were considered to be the period of greatest constancy in composition (Lilleland and Brown, 1941). McCollam (1943, 1944) found that in the vine, citrus and peach the middle of the growing season was the best period for taking leaf samples, since earlier the mineral content tended to be uniformly high,

and later uniformly low. Baker (1943) and Goodall (1945a), however, shewed that the differences in potassium content of apple leaves are more marked in September than at flowering time, and Goodall (1945) also found that the differences in magnesium content between leaves from deficient trees and from others absorbing adequate magnesium increased from July to October. Drosdoff (1944) in tung likewise found the differences in potassium content of the leaves greater in October than in July or August. In respect of nitrogen content, Nasharty (1944) found that differences in peach leaves increased during April and May ; but the data of Frear and Anthony (1943) suggest that the nitrogen concentration in apple leaf samples taken in May may indicate the nutritional status of the trees better than ones taken later.

Many investigators have avoided the selection of the most appropriate time of sampling by taking samples on several occasions through the season. This procedure reduces the risk that effects of differences in the seasonal course of nutrient supply may pass unnoticed (Epstein and Lilleland, 1942), but it may considerably increase the difficulties of interpreting the results. The " foliar diagnosis " school have on several occasions (Lagatu and Maume, 1924, 1924a ; Thomas, 1938b ; Thomas and Mack, 1939c) suggested that optimal nutrition is associated with a linear course of change during the growing season in the proportions between the bases potassium, calcium and magnesium in the leaves. The same idea has also been extended (Lagatu and Maume, 1925 ; Thomas *et al.*, 1944) to the proportion of nitrogen to phosphorus. In spite of the fact that the taking of several successive samples is a central feature of the " foliar diagnosis " technique, its advocates have often been content to report only the mean values for these successive samples, and have even admitted that a single sample may often give sufficient information (Thomas *et al.*, 1942). Analysis of samples taken on several successive occasions may, however, be essential if such analyses are to be used to determine the date and amount of fertilizer applications during the growing season. Proposals of this sort have been made for sugar cane by Yuen and Hance (1939) among others, for tomato by Emmert (1941, 1942a), for pineapple by Nightingale (1942, 1942a), and for grapefruit by Finch (1944) and Jones (1944).

ORGAN OF PLANT TO BE SAMPLED

The possibility cannot be excluded that analysis of the whole plant would provide the best index of nutritional status. It has, indeed, often been argued that, since the plant consists of organs differing greatly in composition, the effect of variation in the proportion of the plant formed by the various organs will be eliminated by confining the analysis to a particular organ, and thus the accuracy of estimation will be increased (Heinrich, 1882 ; Atterberg, 1901 ; Alway, 1928). It must be remembered, however, that the proportion of the different organs is itself affected by the nutritional status of the plant; hence it is hardly possible by such facile, *a priori*, arguments to reject analysis of the whole plant in favour of analysis of separate organs—it is a question which should be resolved by direct experimentation.

Attempts have also been made to select single organs on a basis of *a priori* considerations. It has been reasoned, for instance, that the conducting tissue, since its composition is likely to be closely related to the current nutrient intake of the plant, is also likely to provide the best index of response to immediate nutrient application. The view that the composition of the tracheal sap is related to current nutrient supplies is undoubtedly correct, but to argue from this that it also provides the best index of response can be little more than guessing, and in many cases may be untrue. It has also been argued that, since the leaves are the organs of active assimilation, their composition must be the best basis for estimating the nutritional status of the whole plant.* But nutrition can affect the growth and yield of the plant in many other ways than by direct effects on assimilation, important as these may sometimes be—and even where an unsatisfactory nutritional condition affects the yield by reducing the assimilation, it is quite

* For instance, " In the life of a growing cane crop, from its earliest stages to its maturity, the major chemical activity in the plant takes place within the leaf tissue. It was believed, therefore, that absorption of plant nutrients from the soil by the crop should be reflected from time to time by changes in the relative or total amounts of absorbed nutrients and moisture found in the leaf tissue of the plant." (Hance, 1937). " The leaf is usually considered best because it is such a vital part of the plant in its nutritional processes. It is in the leaf that the plant foods are gathered and combined for redistribution throughout the plant." (McCollam, 1944).

conceivable that analysis of some other part or of the plant as a whole would provide a more sensitive index of the nutrition than analysis of the leaf itself.

When experimental evidence has been brought forward to support the choice of one or other organ for sampling for diagnostic purposes, it has generally been on a basis of proportional (or absolute) differences between plants at different levels of nutrition. For instance, for the diagnosis of boron deficiency in apples, fruits are preferred to leaves for this reason (Askew and Thomson, 1937). Brandenburg (1939) found leaves of beet preferable to roots in this respect, and Burkhart and Page (1941) found the range of calcium concentration in the hot water extracts of peanut material from fertilizer trials to be greatest in the middle and lower leaf blades, that of potassium in the younger petioles, and that of magnesium in the older petioles; it is interesting to note that a similar argument was used by Heinrich (1882—see pp. 12, 13) to support his practice of sampling cereal roots. Sometimes even the low percentage content of a nutrient element in an organ has been cited as an argument against its use—for instance, that of nitrogen in the leaf sheaths of sugar cane by Clements and Moriguchi (1942) and potassium in the grain of oats by Atterberg (1888, 1889); this consideration is valid when only an insensitive method of analysis is available, otherwise it implies that the errors of the analytical results between replicate samples are similar for all organs irrespective of their mineral content.

Where data are available on the variability of analytical results for different organs, a more satisfactory basis exists for the choice of one or other organ for diagnostic purposes. The data of Bartholomew *et al.* (1933), for instance, shew that both the extent and the significance of differences in nitrogen content of tomato plants with varying nitrogen supply are greater in the stems than in the leaves. Ulrich (1942, 1942a, 1942b) found that, in the grape vine, both the potassium and nitrate concentrations in the petioles varied more with varying nutritional conditions than in the leaf-blades, and moreover these differences were more highly significant; hence the petioles were regarded as providing more satisfactory material for diagnostic purposes. Harrington (1944) obtained similar data supporting the use of petioles rather than leaf laminae of spinach for diagnosis of the nutritional status with regard to the three principal nutrients, and also found that the response to a change in supply was more prompt in the petioles. In pecan leaves, on the other hand, Gossard (1943) found that not only was the nitrogen content lower in the rachis than in the leaflets, but also its coefficient of variation was greater and the proportional difference between samples from areas of different nutritional status was less; these lines of approach thus rightly led to the choice of leaflet rather than rachis samples for the diagnosis of nitrogen deficiency.

When the general type of organs to be sampled has been decided, leaves, stems, or petioles, it remains to be considered how accurately the sample type needs to be defined—whether, for example, a leaf at a particular morphological level should be selected, as is done by the "foliar diagnosis" school (see p. 41), whether all the leaves of a certain number of plants should be gathered, as is done by Lundegårdh (1941), or whether a random sample of the leaves should be taken. Since differences in age and morphological position have been shewn to be accompanied by considerable differences in composition, it seems probable that random sampling will be unsatisfactory since these differences will unnecessarily be included among the sources of error. In his study of the nitrogen content of pecan leaves, Gossard (1943) confirmed that the error of random samples of leaves was greater than that of samples selected on criteria of morphological position, size and age. On the other hand, although Wallihan (1944) found differences in composition between different types of leaves in the sugar maple, he considered a random sample from the most accessible part of the crown would be as representative as any planned selection of leaves. Where the age of leaves (or other organs) to be sampled for analytical diagnosis of a particular deficiency is in question, knowledge of the mobility or immobility of the nutrient within the plant may be usefully applied. If it is known that under conditions of deficiency an element is readily remobilized from the older parts to supply the needs of the newly developing organs, there is a reasonable probability that the former will provide better indices of deficiency (Remy, 1903, 1903a; Nightingale, 1942a). This is outstandingly the case with potassium, and less markedly so with nitrogen and phosphorus. Calcium and boron, on the other hand, are not at all readily remobilized, and hence differences in the current ability of the plant to respond to these elements may be more markedly reflected in the composition of the younger parts. As

between different organs of the same type, those which first shew symptoms of deficiency are likely to be those shewing the greatest variations in composition with differences in nutrient supply—thus, symptoms of potassium deficiency generally appear earliest and most clearly on the older leaves, those of boron deficiency in the apical regions (Hambidge, 1941).

In considering which of the various petioles of a sugar beet plant to sample for diagnostic purposes, Brown (1943) used an argument analogous with that of Burström (1937) in relation to the time of sampling; since the variations in petiole composition with position in the crown were least in the leaves of medium age, and since in their selection the personal factor in sampling would thus be least important, these were considered the most suitable for sampling. Similarly, Lineberry *et al.* (1944) preferred mature leaves of strawberries to younger leaves of either crown or runners, because it would be difficult to eliminate the effect of age differences in the latter.

Roach (1945) has put forward, in favour of sampling younger rather than older leaves, the argument that they will be freer from contamination, which may be of importance where certain trace elements are concerned. He also suggested that, by taking samples of young leaves at a constant stage of development, difficulties arising through differing age of leaves at different times in the growing season could be eliminated; however, Richards (1932) has shewn that successive leaves of barley, sampled at the same stage of development, differ greatly in potassium content.

In trees, not only does the question of leaf age arise, but also the morphological position of the leaves to be sampled; the two are to some extent related. Among the investigators who have analysed different morphological types of tree leaves, and have found differences in their composition are Larson (1933), Warne (1934), Fudge (1938, 1939), Kidson *et al.* (1940), Wallace (1940), Reuther and Boynton (1940), Chapman (1941), Goodall (1943, 1945, 1945a) and Wallihan (1944). Sometimes these differences may be ascribed to the proximity of developing fruit (Larson, 1933; Fudge, 1938, 1939), but more often they are associated with differences in leaf age. Kidson *et al.* (1940) found that the range of magnesium content in apple trees showing various degrees of magnesium deficiency was greater in the lower than the upper leaves of the leader shoots. Goodall (1943) found that the proportional difference in potassium content between apple trees differing in potassium status was greater in spur than shoot leaves sampled in the autumn.

If the plant shews deficiency symptoms on some of its leaves only, the question may be put whether such leaves or others which appear healthy should be preferred for diagnostic purposes. There is some evidence (Parbery, 1935; Hardy, 1937; Boresch, 1938; Fudge, 1938, 1939; McGeorge, 1939; Reuther and Boynton, 1940; Southwick, 1943; Goodall, 1945) that in such cases the concentration of the deficient nutrient is lower in the affected leaves than in others from the same plant, though it is not clear in all these investigations that the leaves were comparable in age and morphological position. The concentration of other nutrients in the leaf may, however, also be affected by the presence of deficiency symptoms (Goodall, 1945), which suggests that to restrict the sample to healthy leaves, as has frequently been done (Reuther and Boynton, 1940; Drosdoff and Painter, 1942; W. A. Roach, private communication) may sometimes prevent a mistaken diagnosis.

Some investigators have recommended sampling only part of the leaf lamina. In Hawaii, several investigations on sugar-cane (Hance, 1937; Nishimura and Hance, 1938; Yuen and Hance, 1939; Borden, 1942, 1944; Chem. Dept., Exp. Sta., H.S.P.A., 1944; Doi, 1944) have involved the use of a leaf punch, to remove small discs of tissue from a number of leaves; a leaf punch has also been used by the Montpellier workers on grapevine leaves (Lagatu *et al.*, 1932). This is a very convenient method of taking samples, but the danger of contamination must be remembered if the material is to be used for trace element determination. Emmert (1931) has presented some evidence that in lettuce the composition of the leaf edge reflects the nutritional status of the plant better than that of the more central part of the lamina. In the pineapple, as already mentioned, Nightingale (1942, 1942a) sampled only the meristematic bases of the leaves. In general, however, it is doubtful whether such refinements as restricting the sample to a particular part of the lamina are worth while, especially if slight variation in the line of separation may alter the proportion of tissues and hence the percentage of nutrients in the sample.

The optimum type of sample may not be independent of varying external conditions. Since

changes in light, temperature and water supply affect the distribution of nutrients among the organs, they may result in one organ providing a more reliable type of sample in one year, another in the following year. Hence, where possible, it is desirable to base deductions as to the optimum type of sample on observations in several years or under a wide range of conditions. The optimum type of sample at different stages of development may well not be the same (Gilbert and Hardin, 1927). Drake and Scarseth (1940) have shewn that the distribution of potassium in the tobacco plant is such that the younger leaves provide a better index of differences in the level of supply when it is low, while at higher levels the older leaves give more reliable indications; similarly the data of Gauch and Wadleigh (1945) with kidney bean shew that the increases in sodium content with increasing additions of sodium chloride to the medium are more marked in the roots at lower levels of supply, but in the stems at higher levels. Thus a single type of sample cannot be universally optimal, and it is probably hardly worth while to go to great trouble to identify its optimum.

There is in the literature a fair amount of data on the composition of different organs under varying nutritional conditions, with the yield responses of similar plants to fertilizer treatment. Recalculation from such data would sometimes enable a decision to be reached on which organ should be sampled without recourse to *ad hoc* experimentation—though always with the reservation mentioned above (p. 62) in relation to annual crops, that the yield response of a plant can never be a sure guide to the response of the same species when grown on the same site later. Among the sources of such data may be mentioned Stahl-Schröder's (1904) experiments with oats, Ames's (1910) experiments with wheat, those of Pfeiffer *et al* (1912) on the nitrogen nutrition of oats, the very extensive observations of Wagner (1915) on barley, mangold, oats, rye, sugar beet and wheat, Münter's work on wheat (1919) and sugar beet (1920), and, more recently, the experiments of Chapman (1935) on phosphorus nutrition of oats and of Lorenz (1942) on boron nutrition of beet.

Very much more abundant in the literature are data which enable comparisons to be made of the differences in composition of different plant organs with varying levels of nutrition. Unfortunately, only too rarely are the analytical results from replicate samples (or the errors between them) reported—very commonly, samples from replicate plots in a manurial trial are bulked for the purpose of analysis. Consequently, to most of these data the more satisfactory test of the coefficient of variability of the differences (p. 62) cannot be applied. In Table IV are indicated the organs of many crop plants in which the proportional differences in content (usually on a dry matter basis) of a given nutrient with varying supply of it have been found greatest. Only those sets of data are included in which the differences between organs are marked and tolerably consistent, and where the differences are reasonably ascribable to varying supply of a single nutrient; in some cases this difference is indicated only by the presence or absence of symptoms.

Table IV.

Data relevant to the selection of organs for analytical diagnosis.

N.B.—Letters in brackets refer to Notes at end of Table.

Plant	Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference
APPLE (*Pyrus malus*, etc)					
	N	————	Leaves	Terminal shoots, fruit pulp	Wallace, 1930, 1938
	N	————	2-year twigs	Leaves, 1-year twigs	Gildehaus, 1931
	K	————	Leaves	Twigs, fruit pulp	Wallace, 1929a
	K	————	Leaves	Twigs	Gildehaus, 1931
	K	Various	Leaves	Bark	Chandler, 1936
	K	Late autumn	Leaves	Bark	Batjer & Degman, 1940
	K	Sept.	Spur leaves	Shoot leaves	Goodall, 1943
	Mg	Feb.-Mar. (C).	Older leader leaves	Leader tip leaves	Kidson *et al.*, 1940a; N.Z. Dep. sci. industr. Res., 1942
	B	Harvest	Fruit	Leaves	Ferguson & Wright, 1940; Batjer & Haller, 1942

Plant	Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference.
APRICOT (*Prunus armeniaca*)					
	B	Oct.	Bark	Leaves, wood	Eaton, F. M., 1935
	B	———	Fruit	Leaves, twigs	Eaton, *et al.*, 1941
	Zn	Sept.-Oct.	Stems	Leaves	Chandler *et al.*, 1940
BARLEY (*Hordeum vulgare*)					
	P	Harvest	Straw	Grain	Godlewski, 1901; Hall, 1905; Wagner, 1915
	K	Harvest	Straw	Grain	Godlewski, 1901; Hall, 1905; Wagner, 1915
BEET (*Beta vulgaris*) [*see also* Mangold, Sugar Beet]					
	K	Harvest	Tops	Roots	Lorenz, 1942
	Ca	Harvest	Petioles	Leaves, roots	Lorenz, 1942
	B	Harvest	Tops	Roots	Lorenz, 1942; Binnie, 1943; Gum *et al.*, 1945
	B	Apr.-Aug.	Leaf laminae	Roots	Eaton, 1944
BLACKBERRY (*Rubus* spp.)					
	B	Nov.	Leaves	Stems, roots	Eaton, 1944
BUCKWHEAT (*Fagopyrum esculentum*)					
	P	47 days from germination	Stems (D)	Leaves (D)	Neller, 1935
CABBAGE (*Brassica oleracea*)					
	B	Apr.	Outer leaf laminae	Inner leaf laminae	Eaton, 1944
CAULIFLOWER (*Brassica oleracea*)					
	B	———	Leaves	Stems, heads, roots	Wolf, 1940
CELERY (*Apium graveolens*)					
	P	Autumn	Stalks (D)	Leaves (D)	McCool & Weldon, 1928
	K	Autumn	Stalks (D)	Leaves (D)	McCool & Weldon, 1928
	B	Oct.	Leaves	Crowns, roots	Maier, 1943
CHICORY (*Cichorium intybus*)					
	B	———	Tops	Roots	Muhr, 1942
COFFEE (*Coffea* sp.)					
	B	———	Old leaves	Young leaves	Tanada & Dean, 1942
COTTON (*Gossypium* spp.)					
	N	Various	Leaves	Flower buds	Crowther, 1936a
	K	10 weeks	Lower leaves	Upper leaves, bark	Phillis & Mason, 1940
	B	Nov.	Leaves	Stems, roots	Eaton, 1944
CUCUMBER (*Cucumis sativus*)					
	Mg	———	Lower leaves	Upper leaves, stems, fruits	Carolus, 1935
ELM (*Ulmus americana*)					
	B	Nov.	Leaves	Stems, roots	Eaton, 1944
FIELD BEAN (*Vicia faba*)					
	B	Harvest	Fruit wall	Foliage, seeds	Truninger, 1944a
	Mn	Harvest	Leaves	Seeds	Marsh & Powers, 1945
FIG (*Ficus carica*)					
	B	Nov.	Leaves	Roots	Eaton, 1944
FLAX (*Linum usitatissimum*)					
	P	Harvest	Stems	Seeds	Maschhaupt, 1922
	K	Harvest	Stems	Seeds	Maschhaupt, 1922
	Mg	Harvest	Straw	Seeds	Truninger, 1944

Plant	Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference.
FRENCH BEAN (*Phaseolus vulgaris*; [*see also* Snap Bean]					
	B	Harvest	Foliage	Seeds	Truninger, 1944a
GOOSEBERRY (*Ribes grossularia*)					
	Ca	————	Stems	Leaves, roots	Gauch & Wadleigh, 1945
	K	June	Leaves	Stems, fruit	Wallace, 1928a
GRAPE (*Vitis vinifera* etc)					
	N	————	Leaves	Wood, fruit juice, fruit pulp	Wagner, 1907
	N	May-Sept.	Petioles	Leaf laminae	Ulrich, 1942a
	K	————	Leaves	Wood, fruit juice, fruit pulp	Wagner, 1907
	K	May-Sept.	Petioles	Leaf laminae	Ulrich, 1942, 1943
	B	Nov.	Leaves	Stems	Eaton, 1944
HOP (*Humulus lupulus*)					
	N	June-Sept.	Leaves	Stems	Schneider, 1905
JAPANESE MILLET (*Echinochloa frumentacea*)					
	Mg	9 weeks	Leaves	Stems, roots, heads	Lutman & Walbridge, 1929
KIDNEY BEAN (*see* French Bean)					
KOHLRABI (*Brassica oleracea*)					
	B	Harvest	Leaves	Roots	Truninger, 1944a
LEMON (*Citrus limonia*)					
	P	Winter	Roots	Leaves, stems	Haas, 1936
	Fe	————	Leaves	Stems, roots	Chapman *et al.*, 1940
	Ga	Aug.	Roots	Leaves, stems	Liebig *et al.*, 1943
	In	Aug.	Roots	Leaves, stems	Liebig *et al.*, 1943
LUCERNE (*Medicago sativa*)					
	K	————	Leaves	Stems	Davies, 1940
	S	————	Leaves (with fine stems)	Stems	Alway, 1928
	B	Second cutting	Leaves	Stems	Brown, 1940
	B	July-Sept.	Leaves	Stems, roots	Eaton, 1944
LUPIN (*Lupinus luteus*)					
	Fe	Various	Roots	Tops	Scholz, 1933
MAIZE (*Zea mays*)					
	P	Harvest	Stems	Roots	Craig, 1934b
	K	Flowering	Stems	Leaves	Bartholomew & Janssen, 1929
	Mg	————	Lower leaves	Upper leaves, stems	Garner *et al.*, 1930
	Mg	Harvest	Leaves	Stems, grain	Truninger, 1944
	Fe	June	Roots	Leaves, stems	Olsen, 1938
MANGOLD (*Beta vulgaris*)					
	N	Harvest	Roots	Leaves	Wagner, 1915
	P	Harvest	Roots	Leaves	Wagner, 1915
	K	Harvest	Roots	Leaves	Wagner, 1915
	K	Harvest	Foliage	Roots	Maschhaupt, 1934
	B	————	Leaves	Roots	Brandenburg, 1939
	B	————	Tops	Roots	Muhr, 1942
MUSTARD (*Brassica* spp.)					
	B	Harvest	Straw	Seeds	Truninger, 1944a
OATS (*Avena sativa*)					
	N	Harvest	Straw	Grain	Atterberg, 1887
	N	Harvest	Grain	Straw	Wagner, 1915
	P	Harvest	Straw	Grain	Atterberg, 1887; Wagner, 1915
	P	Heading and ripening	Lower stems (E)	Upper stems (E)	Chapman, 1935

Plant	Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference
OATS (*Avena sativa*)—continued					
	P	Harvest	Straw and chaff	Grain	Opitz, 1944
	K	Harvest	Straw	Grain	Atterberg, 1887, 1901; Wagner, 1915; Ehrenburg, 1919
	K	Harvest	Straw, roots	Grain	Stahl-Schröder, 1904
	Ca	Harvest	Leaves	Grain	Lundegårdh, 1932
	Ca	4-8 weeks	Roots	Leaves, stems	Burström, 1934
	Mg	Harvest	Straw	Grain	Atterberg, 1887; Truninger, 1944
	Mn	6 weeks	Roots	Tops	Burström, 1934
ONION (*Allium cepa*)					
	B	Apr.-Sept.	Leaves	Roots	Eaton, 1944
	Mn	Harvest	Outer skin of bulb	Inner part of bulb	Muckenhirn, 1936
ORANGE (*Citrus aurantium*, etc)					
	N	————	Roots	Stems, leaves	Chapman & Liebig, 1940
	P	July	Stems, older roots	Leaves, fine roots	Chapman & Brown, 1941
	Ca	Feb.	Leaves	Stems, roots	Reed & Haas, 1923
	S	————	Leaves	Stems, rootlets	Haas, 1936b
	S	July	Stems, older roots	Leaves, fine roots	Chapman & Brown, 1941a
	B	Various	Leaves	Fruit	Morris, 1938
PEA (*Pisum sativum*)					
	P	July	Leaves and stems	Fruit	Opitz, 1944
	K	Harvest	Foliage	Seeds	Maschhaupt, 1934
	B	Harvest	Foliage	Fruit walls, seeds	Truninger, 1944a
PEACH (*Prunus persica*)					
	N	June-Aug.	Fruit flesh	Endocarp, seeds	Lott, 1942
	B	Nov.	Roots	Leaves, stems	Eaton, 1944
PEANUT (*Arachis hypogaea*)					
	P	Harvest	Fruit walls	Seeds	Burkhart & Collins, 1942
	K	Harvest	Fruit walls	Seeds	Burkhart & Collins, 1942; Collins & Morris, 1942
	Ca	Harvest	Fruit walls	Seeds	Collins & Morris, 1942
	Mg	Harvest	Fruit walls	Seeds	Collins & Morris, 1942; Burkhart & Collins, 1942
PEAR (*Pyrus communis*)					
	N	Sept.-Oct.	Leaves	Stems, roots, fruit	Wagner, 1931
	K	Sept.-Oct.	Leaves, twigs	Older stems, roots, fruit	Wagner, 1931
	B	————	Leaves, twig bark	Twig wood	Eaton *et al.*, 1941
PECAN (*Carya pecan*)					
	Zn	Aug.	Petioles, stems	Leaf laminae	Finch & Kinnison, 1936
PERSIMMON (*Diospyros Kaki*)					
	B	Nov.	Leaves	Stems, roots	Eaton, 1944
PINEAPPLE (*Ananas sativus*)					
	B	————	Leaf tips	Other organs	Dean & Tanada, 1943
	Zn	————	Stem growing point	Other organs	Lyman & Dean, 1942; Dean & Tanada, 1943
PLUM (*Prunus domestica*)					
	K	————	Leaves	Fruit pulp	Lilleland, 1951; Wallace, 1931; Wallace & Prebsting, 1933
	B	Oct.	Stems	Leaves	Eaton, F. M., 1935; Eaton *et al.*, 1941
	Cu	Late midsummer	Leaves	Stems	Anderssen, 1932

Plant	Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference.
POTATO (*Solanum tuberosum*)					
	N	5-13 weeks from planting	Petioles, stems, tubers, roots	Leaf laminae	Lorenz, 1944
	N	9-13 weeks from planting	Petioles, stems, tubers, roots	Leaf laminae	Lorenz, 1944a
	P	5-13 weeks from planting	Roots	Leaf laminae, petioles, stems, tubers	Lorenz, 1944
	K	Harvest	Tops	Tubers	Metz, 1923
	Mg	————	Leaves	Tubers	Garner *et al.*, 1930
	Mg	————	Lower leaves	Upper leaves	Carolus, 1934
	B	May	Leaves	Tubers	Eaton, 1944
	[illegible]	Harvest	Outer skin of tubers	Inner part of tubers	Muckenhirn, 1936
	Cu	Jan.-Mar. (C)	Leaves	Tubers	Teakle, Morgan & Turton, 1941
RADISH (*Raphanus sativus*)					
	B	62 days	Leaves	Roots	N.J. agric Exp. Sta., 1939
	B	————	Tops	Roots	Muhr, 1942; Tanada & Dean, 1942
	B	Various	Leaves	Roots	Eaton, 1944
RED CLOVER (*Trifolium pratense*)					
	Ca	————	Tops	Roots	DeTurk, in Hambidge, 1941
	B	Harvest	Straw	Seeds	Truninger, 1944a
RED CURRANT (*Ribes sativum*)					
	K	July	Leaves	Stems	Wallace, 1929b; Wallace & Proebsting, 1933
RED PEPPER (*Capsicum frutescens*)					
	Mg	————	Leaves	Fruit	Carolus, 1935
	B	Oct.	Leaves	Fruit.	Eaton, 1944
RICE (*Oryza sativa*)					
	S	Dec.-Jan.	Straw	Grain	Sen, 1938a; Aiyar, 1945
	Cu	————	Grain	Straw, roots	Tokuoka & Dyo, 1938
RUTABAGA (*Brassica* sp)					
	Ca	Harvest	Tops	Roots	Beaumont & Snell, 1935
	Mg	Harvest	Tops	Roots	Beaumont & Snell, 1935
RYE (*Secale cereale*)					
	P	Harvest	Straw	Grain	Wagner, 1915; Alway *et al.*, 1926
	K	Harvest	Straw	Grain	Wagner, 1915
SNAP BEAN (*Phaseolus vulgaris*) [*see also* French Bean]					
	Mg	————	Leaflets	Petioles, stems, fruit	Carolus, 1935
SOYBEAN (*Glycine soja*)					
	Fe	30 days from germination	Roots	Leaves	Somers & Shive, 1942
	Mn	30 days from germination	Roots	Leaves	Somers & Shive, 1942
STRAWBERRY (*Fragaria chiloensis*)					
	P	Fruiting	Leaves	Fruit	Lineberry & Burkhart, 1943
	P	June	Crown leaves (H)	Runner leaves (H)	Lineberry *et al.*, 1944

Plant Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference
SUGAR BEET (*Beta vulgaris*)				
N	Harvest	Roots	Leaves	Wagner, 1915
P	Sept.	Stems (D)	Leaves (D)	McCool & Weldon, 1928
K	Harvest	Foliage	Roots	Münter, 1920
K	Sept.	Stems (D)	Leaves (D)	McCool & Weldon, 1928
K	Harvest	Older leaves	Younger leaves, roots	van Schreven, 1937
Ca	Harvest	Roots	Leaves, crown	Hirst & Greaves, 1944
Na	Harvest	Leaves	Roots	van Schreven, 1937
B	———	Leaves	Roots	Brandenburg, 1939
B	———	Tops	Roots	Muhr, 1942
B	Various	Leaf laminae	Roots	Eaton, 1944
B	Harvest	Leaves	Roots	Try[illegible]944a
Mn	Harvest	Leaves	Roots	de Haan, 1937; Marsh & Powers, 1945
SUGAR CANE (*Saccharum officinarum*)				
N	10-18 months after planting	Lower stems	Leaves, upper stems	Das & Cornelison, 1936
N	———	Lower stems	Leaves, upper stems	Clements *et al.*, 1941
P	———	Lower stems	Leaves, upper stems	Clements *et al.*, 1941
K	———	Older leaves, older stems	Younger leaves, younger stems	Clements *et al.*, 1941
B	———	Leaf laminae	Leaf sheaths, stems	Tanada & Dean, 1942
SUNFLOWER (*Helianthus annuus*)				
Fe	———	Younger leaves	Older leaves	Glenister, 1944
B	Various	Leaves	Stems, roots	Scofield *et al.*, 1940
SWEET POTATO (*Ipomaea batatas*)				
Mg	———	Leaves	Tubers	Garner *et al.* 1930
B	Oct.	Tops	Roots	Eaton, 1944
TEA (*Thea sinensis*)				
P	May	Older leaves	Younger leaves, stems	de Haan, 1941
K	May	Stems	Leaves	de Haan, 1941
Ca	May	Stems	Leaves	de Haan, 1941
TOBACCO (*Nicotiana tabacum*)				
K	Near maturity	Younger leaves (F) Older leaves (G)	Older leaves (F) Younger leaves (G)	Drake & Scarseth, 1940
K	After curing	Older leaves	Younger leaves	Gribbins *et al.*, 1941
Mg	———	Older leaves	Younger leaves, stems	Garner *et al.*, 1930
TOMATO (*Lycopersicum esculentum*)				
N	Blossoming, fruiting	Stems	Leaves	Bartholomew *et al.*, 1933
N	Sept.	Leaves, stems	Roots, fruit	Raleigh & Chucka, 1944
P	Aug.	Lower stems	Upper stems, leaves, fruit, roots	Carolus, 1943a
P	Sept.	Roots	Leaves, stems, fruit	Raleigh & Chucka, 1944
K	April-May	Stems	Leaves	Wall, 1939
K	April-May	Stems	Leaves, fruit	Wall, 1940a, 1940b
K	Sept.	Leaves, stems, roots	Fruit	Raleigh & Chucka, 1944
K	End of season	Lower leaves	Upper leaves	Clarke, 1944
Ca	Sept.	Leaves, stems, roots	Fruit	Raleigh & Chucka, 1944
Mg	Sept.	Leaves, stems	Roots, fruit	Raleigh & Chucka, 1944
Fe	Various	Upper leaflets, fruit	Lower leaflets	Lyon *et al.*, 1943
B	July-Aug.	Leaves	Fruit	Eaton, 1944
Mn	Various	Lower leaflets	Upper leaflets, fruit	Lyon *et al.*, 1943
Zn	Various	Fruit	Leaflets	Lyon *et al.*, 1943
Mo	Various	Lower leaflets	Upper leaflets, fruit	Lyon *et al.*, 1943

Plant	Element	Date or stage of development	(A) (*see* Notes)	(B) (*see* Notes)	Reference.
TURNIP	(*Brassica rapa*)				
	N	Harvest	Roots	Leaves	Wagner, 1915
	K	Harvest	Roots	Leaves	Wagner, 1915
	B	May	Leaves	Roots	Eaton, 1944
WHEAT	(*Triticum vulgare*)				
	P	Harvest	Straw	Grain	Hall, 1905; Wagner, 1915; Maschhaupt, 1921
	P	Harvest	Grain	Straw	Ames, 1910
	K	Harvest	Straw	Grain	Helmkampf, 1892; Hall, 1905; Ames, 1910; Wagner, 1915

NOTES

A. Organ(s) whose percentage nutrient content varied more markedly with increase in nutrient supply.
B. Organ(s) whose percentage nutrient content varied less markedly with increase in nutrient supply.
C. In Southern Hemisphere.
D. Nutrients determined in expressed sap.
E. Percentage content of inorganic phosphate determined.
F. At low level of potassium supply.
G. At high level of potassium supply.
H. Nutrients determined in hot water extract.

It is clear from Table IV that, in the majority of cases for which data are available, the proportional increase in internal concentration of a nutrient with increase in its supply is greater in the leaves than in other organs. Thus, so far as it goes, this evidence supports the broad generalization put forward by Thomas and Mack (1939) and by Wallace (1943) that leaf analysis is to be preferred in diagnostic work.

Those investigators, whose methods involve the analysis of extracts of the plant tissue or sap considered to contain only unelaborated nutrients, have often preferred to sample organs with a large proportion of conducting tissue—stems, petioles or midribs. The few data in Table IV bearing on this point (McCool and Weldon, 1928; Neller, 1935) do, indeed, support this practice. Thornton (1932) stated that the inorganic phosphate content of the translocation and storage tissues was a more sensitive index of phosphorus nutrition than that of the leaves. Emmert (1942a) found that the lower petioles of tomatoes, extracted with 2% acetic acid, were preferable to other organs for the indication of current nutrient supply, because temporary changes in environmental conditions affecting growth rate had less effect on the composition of the extract of these petioles than on that of other organs. An additional reason for choosing organs with little pigmentation for extraction may be that the presence of pigments, tannins, etc. may affect the accuracy and ease of carrying out colorimetric tests (Nicholas and Jones, 1945; A. W. Greenhill, private communication).

It must be remembered that in choosing a type of sample for diagnostic purposes it may be necessary in practice to use the same sample for determination of several nutrients. In other words, a compromise must be effected, and a sample giving reasonable indications of the status of all nutrients under study selected rather than a type of sample most appropriate for one nutrient but unsatisfactory for others.

The actual sample types chosen by certain investigators may be seen in Tables II, XII and XV; types used by other investigators who have carried out systematic work in this field but who have not proposed any numerical limiting values or ratios are shewn in Table V unless mentioned elsewhere in this section.

Table V

Material used or recommended for diagnostic purposes in investigations other than those mentioned in Tables II, XII and XV.

Plant	Elements	Time or stage of development	Part sampled	Reference
APPLE (*Pyrus malus*, etc.) [*see also* Deciduous fruits]				
	General	———	Middle shoot leaves	Boynton & Compton, 1944; Boynton, 1945
	General	July-Sept.	Petioles near base of leader growth	Nicholas & Jones, 1945
	General	———	Terminal 5″ of twig	Davidson, in Hambidge, 1941
	N	———	Middle shoot leaves	Baker, 1936, Haas *et al.*, 1940; Smock & Boynton, 1944
	K	Various	Middle shoot leaves	Baker, 1941; Boynton *et al.*, 1941; Boynton & Cain, 1942
	K	———	Leaves	Reuther, 1941
	K	Various	Petioles	Potter & Percival, 1938
	Mg	Jan.-Feb.	Lower leader leaves	Kidson *et al.*, 1943
	Mg.	Various	Leaves	Southwick & Shaw, 1944; Southwick & Smith, 1945
BARLEY (*Hordeum vulgare*) [*see* Small Grains]				
BEET (*Beta vulgaris*)		[*see also* Sugar beet]		
	K	———	Roots	Gilbert, 1926
	B	———	Leaves	Berger & Truog, 1940
CABBAGE (*Brassica oleracea*)				
	N	———	Midribs	Gilbert, 1926
	N, P	———	Midribs	Emmert, 1935b
	P	Beginning of head formation	Lower part of stem	Thornton, 1932
CACAO (*Theobroma cacao*)				
	General	Various	Leaves from most recent growth flush	McDonald, 1933
CAULIFLOWER (*Brassica oleracea*)				
	General	Oct.	Midrib of first upright leaf.	Nicholas & Jones, 1945.
CELERY (*Apium graveolens*)				
	K	———	Stems	Gilbert, 1926
CITRUS (*Citrus* spp.)		[*see also* Grapefruit, Orange]		
	General	June-July*	Leaves from fruit stalk against fruit	Bathurst, 1943
	General	May-July*	Leaves from growth flush at time of setting main crop	Bathurst, 1944a
	N	———	Mature leaves	Hilgeman *et al.*, 1940
	Mg	April	Spring flush foliage	Fudge, 1942a
CLOVER (*Trifolium* spp.)		[*see also* Legumes, Subterranean Clover]		
	P	———	Growing tips of main stems	Thornton *et al.*, 1934
	K	———	Main stems	Thornton *et al.*, 1934
DECIDUOUS FRUITS [*see also* Apple, Peach, Plum]				
	General	———	Leaves from lower part of current season's growth.	McCollam, 1944

*In Southern Hemisphere.

Plant	Element	Time or stage of development	Part sampled	Reference
GRAPE (*Vitis vinifera*)				
	General	———	Recently matured leaf some distance from tip of new cane	McCollam, 1944
GRAPEFRUIT (*Citrus paradisi*) [*see also* Citrus]				
	N	———	Leaves, twigs	Martin, 1940
HOP (*Humulus lupulus*)				
	General	Aug.	Petioles from mid-stem region	Nicholas & Jones, 1945
LEGUMES (*see also* Clover, Lima Bean, Lucerne, Pea, Snap Bean, Soya Bean, Subterranean Clover, White Bean)				
	K	———	Tips of main stems	Thornton, 1933a
LETTUCE (*Lactuca sativa*)				
	N, P	Various	Older midribs	Emmert, 1934
	K	———	Leaves	Gilbert, 1926
LIMA BEAN (*Phaseolus lunatus*) [*see also* Legumes]				
	N, P	———	Main stem	Emmert, 1935b
LUCERNE (*Medicago sativa*) [*see also* Legumes]				
	P	Before blossom formation	Growing tips of main stems	Thornton, 1932; Thornton *et al.*, 1934
	K	———	Main stems	Thornton *et al.*, 1934
MAIZE (*Zea mays*)				
	General	Various	Third leaf from base	Thomas, 1938b; Thomas & Mack, 1939, 1939a, 1939b, 1939c, 1939e, 1943; Thomas *et al.*, 1943
	General	Various	Fourth leaf from base	Thomas *et al.*, 1944
	N	———	Stem internodes	Gilbert, 1926
	N	———	Bases of main stems	Thornton *et al.*, 1934
	P	Between tasselling and silking	Main stems, just below tassel	Thornton, 1932; Thornton *et al.*, 1934
	P	———	Stem tips	Gilbert, 1926
	K	———	Base of leaf at ear node	Thornton, 1933a; Thornton *et al.*, 1934
OATS (*Avena sativa*)		[*see* Small Grains]		
ONION (*Allium cepa*)				
	General	———	Leaf bases	Plant *et al.*, 1945
ORANGE (*Citrus aurantium*, etc.) [*see also* Citrus]				
	General	———	Leaf from spring cycle of growth, just behind a small green fruit.	McCollam, 1944
PEA (*Pisum sativum*) [*see also* Legumes]				
	N, P, K	Various	Stem	Wolf, 1945
PEACH (*Prunus persica*) [*see also* Deciduous fruits]				
	General	———	Terminal 6" of twig	Davidson, in Hambidge, 1941
	N, P, K	Various	Leaves	Waugh & Cullinan, 1941
	N, P	Dormant season	Twigs	Waltman, 1944
	N, P	———	New shoots, growing tips	Emmert, 1935b
	P, K	———	Leaves	Lilleland, 1933
	P, K	June, July	Basal leaves of current season's growth	Lilleland & Brown, 1941, 1942
	K	Various	Terminal leaves	Baker, 1941

Plant	Element	Time or stage of development	Part sampled	Reference
PINEAPPLE (*Ananas sativus*)				
	N	Various	Leaf bases	Tam & Clark, 1943
PLUM (*Prunus domestica*) [*see also* Deciduous fruits]				
	K, Ca, Mg	Various	Leaves	Hoagland & Chandler, 1933
	K	Aug.-Sept.	Middle shoot leaves	Boynton *et al.*, 1941
POTATO (*Solanum tuberosum*)				
	General	Various	4th-11th leaves from base of primary stems	Thomas & Mack, 1938
	General	July-Aug.	Petioles from mid-stem region	Nicholas & Jones, 1945
	N, P, K	Early stages of tuber development	Main stem near ground	Thornton, 1932, 1933a; Thornton, *et al.*, 1934
	N, P, K	Various	4th or 5th leaves from base of primary stems	Thomas, 1936, 1937, 1938, 1938a; Thomas & Mack, 1939c, 1939d, 1939f
	N, P	———	Lower main stems	Emmert, 1937
	P, K	———	Leaf nearest inflorescence	Sandrock, 1931
RASPBERRY (*Rubus idaeus*)				
	K	Autumn	Leaves	Darrow & Magness 1939
RUBBER (*Hevea brasiliensis*)				
	N, P, K	Dormancy	Largest leaf laminae of whorl	Chapman, 1941
RYE (*Secale cereale*) [*see* Small Grains]				
SMALL GRAINS [*see also* Wheat]				
	N	———	Main stems	Thornton *et al.*, 1934
	P	"Jointing"	Growing tips of main stems	Thornton, 1932; Thornton *et al.*, 1934
	K	———	Bases of leaves near middle of main stems	Thornton, 1932a; Thornton *et al.*, 1934
SNAP BEAN (*Phaseolus vulgaris*) [*see also* Legumes]				
	General	Various	Basal leaves	Thomas *et al.*, 1942
SOYA BEAN (*Glycine soja*) [*see also* Legumes]				
	P	———	Growing tips of main stems	Thornton *et al.*, 1934
	K	———	Main stems	Thornton *et al.*, 1934
SPINACH (*Spinacia oleracea*)				
	N, P, K	———	Petioles	Thornton *et al.*, 1934
	K	———	Leaves	Gilbert, 1926
SUBTERRANEAN CLOVER (*Trifolium subterraneum*) [*see also* Clover, Legumes]				
	Mo	Beginning of flowering	Leaves	Teakle, 1944
SUGAR BEET (*Beta vulgaris*) [*see also* Beet]				
	General	———	Leaves midway between old outer leaves and small immature ones	McCollam, 1944
	General	Aug.	Midrib of first upright leaf	Nicholas & Jones, 1945
	N, P, K	———	Petioles	Thornton, 1932; Thornton *et al.*, 1934
	N	———	Petioles of central leaves	Ulrich, 1941
SUGAR CANE (*Saccharum officinarum*)				
	N, P, K	———	Tops	Hance, 1936
	N, P, K	———	Punch samples from centre region of 3rd-5th leaves from apex.	Hance, 1937

Plant	Element	Time or stage of development	Part sampled	Reference
TOBACCO (*Nicotiana tabacum*)				
	General	Various	Leaves (various levels)	Lagatu & Maume, 1935, 1935a, 1935e, 1936c
	N, P, K	———	Base of midribs from upper part of main stems	Thornton *et al.*, 1934
TOMATO (*Lycopersicum esculentum*)				
	General	Various	Leaves (various levels)	Thomas & Mack, 1941a, 1941b; Thomas *et al.*, 1943a
	General	Oct.-Dec.	Petioles from mid-stem region	Nicholas & Jones, 1945
	N, P, K	———	Petioles from middle of main stem	Thornton *et al.*, 1934
	N, P, K	Various	5th leaf from base	Thomas & Mack, 1940, 1941, 1943a
	N	Various	Older petioles	Emmert, 1934, 1935b
	N	———	Leaves	Gilbert, 1926
TURNIP (*Brassica rapa*)				
	N, P, K	———	Petioles	Thornton *et al.*, 1934
WHEAT (*Triticum vulgare*) [*see also* Small Grains]				
	N, P, K	Earing, flowering	Tops	Maume & Dulac, 1934, 1934a, 1935, 1935a, 1936, 1936a, 1937, 1938, 1938a
	S	Earing, flowering	Tops	Maume & Bouat, 1937
WHITE BEAN (*Phaseolus* sp.) [*see also* Legumes]				
	P, K	———	Leaves	Cook, R. L., 1941

PREPARATION OF MATERIAL FOR ANALYSIS

Cleaning

The first necessity is that the external surface of the material shall be free from contamination, particularly with substances containing the elements under investigation. Where the trace elements are concerned, a very small amount of contamination may contain sufficient completely to invalidate the analytical results.

The most important sources of contamination are soil, atmospheric dust and spray materials. Soil contamination is of course most important for root samples—it has indeed often been a reason for the rejection of root samples as material for diagnostic analysis (Helmkampf, 1892; Stahl-Schröder, 1904)—but it may also be considerable on leaves and stems near ground level. The total content of many of the trace elements (including iron) and also of calcium in soil may be considerably higher than in plant dry matter, and hence soil contamination may result in over-estimation of the content of these elements in the plant material; iron content of dry plant material samples has even been used as an index of soil contamination, and so also has their aluminium content (Piper, 1942a). Atmospheric dust is often similar in composition to soil, but in the vicinity of industrial works it may contain considerable quantities of other materials containing elements of interest in plant nutrition; dust may contaminate all the aerial parts of the plant. Spray residues are an important source of contamination for the fruit, stems and leaves of crops to which sprays are normally applied. They commonly contain calcium, sulphur or copper—all of importance in plant nutrition—and may contain a wide variety of other elements. Lindner (1943) has shewn that spray may carry a considerable distance—at half a mile from the nearest point where an arsenic spray had been used, surface contamination of peach leaves with arsenic amounted to two or three times their normal arsenic content.

The removal of surface contamination from plant material is not a simple matter. Many investigators recommend washing samples with distilled water (Parbery, 1935; Thorne and

Wallace, 1944). This however is liable to cause losses of certain nutrients from the plant material by leaching; this may be particularly serious for potassium—if the leaching is continued long enough, up to 99% of the total potassium in apple leaves may be lost (Mann and Wallace, 1925), and even rain will remove considerable amounts (Richards, 1932; van Schreven, 1938; Albrecht, 1943). Moreover, it is not at all certain how effective washing in distilled water may be for the removal of insoluble surface contaminants. Other workers (Boynton *et al.*, 1944; Goodall, 1943, 1945, 1945a; Bathurst, 1944a; Roach, 1944) have wiped the surface of the organs with muslin or other cloth, or with cotton wool; this avoids the possibility of leaching, but again its effectiveness in removing contamination is open to question. So far as the author is aware, neither of these procedures has ever been tested carefully—neither the amounts removed nor the amounts remaining have been estimated. A test would be possible by artificial contamination with some material not normally present to an appreciable extent in plant tissue—but even then one could never be sure that any amount remaining had not been absorbed by the leaf, and it would be very doubtful whether results obtained could be applied to field conditions.

Lindner (1943) found that washing with water was inadequate to remove arsenic spray residues on peach leaves. Accordingly he dipped the leaves in an alcoholic solution of sodium hydroxide. This technique would probably not be generally applicable. In another investigation, mainly on pear leaves, the same investigator (Lindner and Harley, 1944) first swabbed the leaves with moist cotton and then rinsed in distilled water.

Jacobson (1945) found it necessary to rub leaves intended for iron determinations with 0.3 N hydrochloric acid, in order adequately to remove spray residues and dust.

Drying

When cleaned, it is generally necessary for the material to be dried. Some analytical procedures do indeed demand the use of fresh material, either directly or in the form of an extract or expressed sap (see below); but generally the dried plant material forms the starting point of the analyses, having the important advantage that it can be stored indefinitely if immediate analysis is inconvenient. Unless the material can be killed soon after collection, it is desirable that drying should proceed rapidly, to avoid respiratory losses. Goodall (1945b) has shewn that, in young tomato plants, these commonly lie between 0.2 and 0.5% of the dry weight per hour at moderate temperatures—that is, over a period of twenty-four hours a loss of between 5 and 10% might well take place, resulting in a corresponding increase in the apparent percentage nutrient content. This loss would of course be prevented if the temperature of the material were rapidly raised to a point at which respiration ceased. But the heat distribution in many types of oven is far from uniform, especially when they contain a large bulk of moist material, so that this condition will often not be fulfilled.

The exact temperature of drying is probably not a matter of great importance provided it is standardized; there is little likelihood of appreciable losses of nutrients (except possibly sulphur) if the temperature does not exceed 100°C. Some interconversion of organic compounds of nutrients — particularly nitrogen, phosphorus and sulphur — may occur, but unless the diagnostic analysis is carried out only for one or other of these compounds or groups of compounds such interconversion will not affect the result. As will be shewn later, it has rarely been suggested that analysis for these organically combined fractions would be of greater diagnostic value than the total content of the same nutrient or its inorganic fractions.

It goes without saying that in the drying process the risk of contamination from the material of the oven, or of trays in which the material is placed, should be avoided. If the internal surface of the oven is composed of a metal of interest in plant nutrition as a trace element, there may be a serious risk of minute flakes falling on the samples and causing substantial errors (Piper, 1942a).

Grinding

It is usual to grind the dried plant material before analysis—partly for greater ease in manipulation, partly in order to secure greater uniformity in composition. Very often a mechanical mill is used for grinding, but this may lead to serious contamination with some of the elements present in smaller quantity in plant material. Hood *et al.* (1944) made a careful study of the Wiley mill (using blades), the C and N mill (beater action) and various types of ball mills; they

found that all caused contamination with iron and copper, and the ball mills with other elements besides. If the contamination were constant, allowance could be made for it ; but in fact it was found to be erratic. Piper too (1942a) considered that any steel mill was not permissible for samples intended for iron determination—a bronze C and N mill could be used ; if copper or zinc determinations were to be made the mill should contain no brass, even in parts not coming directly into contact with the material. Drosdoff (1944), on the other hand, found only slight iron contamination from the Wiley mill. Where samples are small, they can generally be ground by hand—preferably in an agate mortar—to avoid contamination (though even small amounts of some types of material, especially cereal stems, are difficult to grind by hand) ; but when there is any considerable quantity of material, hand grinding becomes excessively laborious, and choice must be made between the types of contamination caused by the different mills. By grinding the material separately in different mills for copper and iron determinations, fully satisfactory results should be possible.

THE ANALYSIS ITSELF

Determination of a Nutrient other than that Deficient

The great majority of diagnostic methods involving the use of plant analysis have been based on determinations in the tissues of the element whose status is in question. An outstanding exception was the " stalk-test " method (Hoffer, 1926), extensively used with maize in America for some years. This depended upon the observation by Hoffer and Trost (1923) that under conditions of potassium deficiency accumulations of insoluble iron compounds appeared in the nodes. The test was never intended as any more than a very rough indication of the potassium status of the plants and of the soil in which they were growing, and as such was found useful in a number of investigations ; the agreement with other tests of potassium status was moderate (Eckstein and Jacob, 1929 ; Thornton, 1931 ; Krüger *et al.*, 1931 ; Stewart *et al.*, 1932 ; Pettinger and Thornton, 1934). Other investigators, however, found the test of little value (Welton *et al.*, 1926 ; Salter and Ames, 1928 ; Snell and McKibbin, 1933). Eckstein and Jacob (1929) had suggested that iron accumulation under conditions of potassium deficiency was not confined to maize, but Krüger *et al.* (1931) found the test inapplicable to oats and Neeb (1931) to sugar cane. As direct rapid tissue tests for potassium were developed, this method was gradually abandoned. Among other instances where the concentration in the plant of some substance other than that deficient has been suggested as an index of the deficiency may be mentioned Roach's (1940, 1943) use of calcium content to indicate probable deficiencies of iron and other trace elements, the suggestion from Trinidad (Emp. Cott. Gr. Corp., 1942) that the sugar content of cotton leaves might provide a means of determining their potassium status, and Leeper's (1941) observation that under conditions of manganese deficiency oats and *Phalaris minor* accumulate in their stems large amounts of nitrate.

Determination of the Deficient Nutrient

Where the nutrient whose status is under investigation is itself to be determined in the plant material, the question needs to be raised whether the determination shall be performed on the whole plant material, or upon some extract of it. Since, unless extraction is complete, an extraction technique removes certain chemical fractions preferentially, this problem is closely linked with the question of whether particular chemical fractions of the nutrient should be investigated.

Analysis for Particular Chemical Fractions

It has frequently been claimed that those fractions of the nutrients within the plant which have not yet been built up into its tissues—the " unelaborated" fractions—provide an index of the balance between current uptake of these nutrients and their utilization by the meristems (Carolus, 1938a, Ulrich, 1944)—a better index of current nutrition than the total nutrient content, since the elaborated fractions present mainly in the insoluble part of the plant material tend to form a relatively constant proportion of it (Emmert, 1942). It may be pointed out that the unelaborated fractions of nutrients in many cases do not themselves constitute the materials directly necessary for meristematic activity, and that consequently no direct connection between

the rate of growth of the plant and the concentration of unelaborated nutrients within it can be assumed. There is, however, a not inconsiderable body of evidence to show that the concentrations of the unelaborated fractions of nutrients in the plant indicate their status more clearly than the total concentration of the same nutrients.

NITROGEN. Most of the evidence as to the relative value of elaborated and unelaborated nutrient fractions in plant material as diagnostic indices relates to nitrogen, and particularly to nitrate determinations. Ulrich (1942a, 1942b, 1943), for instance, compared the effect of sulphate of ammonia on the nitrate-nitrogen, total soluble nitrogen, and insoluble nitrogen content of grape petioles and leaf-blades; the proportional effect on the nitrate content of the petioles was larger than on any of the other fractions in petioles or blades, and for the earlier samples the significance of the effect was also greater. His observations (1943, 1943a) on the effect of four levels of nitrogen supply on the nitrogen content of sugar beet are rather more equivocal: he concludes that "the nitrate content of the outside petioles . . . . for June 1 indicated the nitrogen status of the plants better than any other nitrogen fraction," but in fact at that date the significance of the differences observed in the total soluble nitrogen content of the same organs was rather greater than that for their nitrate content.

Most other investigations on the subject relate only to the proportional changes in the various nitrogen fractions in the plant with different nitrogen fertilizer treatment. Cook (1930) found the changes in nitrate content of the sap of oat plants following application of nitrogenous fertilizers were proportionally much greater in most cases than those in the total nitrogen content of the same tissues. Emmert (1931), in experiments in which tomatoes and lettuces were grown in soils varying in reaction, found that the nitrate concentration in the leaves gave better indication of soil nutrient relations than the total nitrogen content, especially in tomatoes. Investigations in Rhode Island (R.I. agric. Exp. Sta., 1933, 1934) showed that in beet and celery the nitrate content of the juice consistently reflected the nitrogen supply level, but that the ammonia content did not. Garner and his collaborators (Garner *et al.*, 1934) analysed tobacco leaves from plants receiving different levels of nitrogen supply for six nitrogen fractions, and found that the nitrate content shewed much greater proportional differences than any other fraction until the flowering stage was reached; in cured leaves (Garner, 1939) the effect of nitrogen supply on nitrate content was less regular than the effect on other nitrogen fractions. Lowry *et al.* (1936), studying the exuded sap of maize in a manurial trial, found that the differences in nitrate content as a result of application of sulphate of ammonia were both more marked and rather more consistent than those in total nitrogen content. Richards and Templeman (1936), in a careful study of the nitrogen metabolism of barley leaves of different ages, found the proportional difference in nitrate content with different nitrogen supply almost invariably greater than in any other of the five nitrogen fractions studied. In cotton plants grown in sand culture and analysed at flowering, Wadleigh (1938) found that nitrogen supply affected the concentration of nitrogen fractions other than nitrate very little though the percentage of nitrate varied greatly with the treatment.

Other workers, on the contrary, have found little reason to prefer the content of nitrate nitrogen as a diagnostic index to that of other fractions. Carolus and his collaborators (Carolus, 1938; Carolus *et al.*, 1938) found that in the 2% acetic acid extract of stems or petioles of potato and cabbage, the nitrate nitrogen and soluble nitrogen content reflected the nitrogen nutrition in very similar fashion. The data of Lorenz and Minges (1942) shewed that, in the 2% acetic acid extract of the midribs of outer leaves from lettuce plants subjected to various nutritional treatments, the proportional differences in nitrate content were only slightly greater than those in total soluble nitrogen.

A few investigators have not determined nitrate nitrogen, but have compared only the soluble and insoluble nitrogen content, or that of protein and non-protein nitrogen. Petrie (1937), for instance, found that in wheat and Sudan grass the proportional increase in soluble nitrogen content with increased nitrogen supply was more marked than that in insoluble nitrogen —at least in the earlier stages of growth; Brown's (1945) data for peach shoots shew the same; Vinall and Wilkins (1936) found changes in non-protein nitrogen in bluegrass more marked than those in protein nitrogen. The Trinidad workers (Phillis and Mason, 1939; Emp. Cott. Gr.

Corp., 1942 ; Mason and Phillis, 1943) considered that nitrogen deficiency should be judged by the concentration of crystalloid rather than protein nitrogen in the leaf of cotton, and shewed that the former varied much more markedly with nitrogen supply than the latter. In his careful study of the nitrogen nutrition of the cotton plant, Wadleigh (1944) concluded that the soluble organic nitrogen content of the main roots was one of the better indices of potential production.

Although much of this evidence supports the view that the content of soluble nitrogen fractions and particularly of nitrate varies more markedly with the changing nutritional conditions than that of the more fully elaborated fractions, there seems to be none demonstrating conclusively that the former provides a better index to expected yield increments with nitrogenous fertilizers. In fact, few data enabling a relationship between yield increments and the content of different nitrogen fractions to be computed appear to be available. Nevertheless, in spite of the paucity of the evidence, many investigators in the field of analytical diagnosis besides those mentioned above have chosen to determine nitrate-nitrogen rather than total nitrogen in their material ; the Purdue University system of tests (pp. 42), for instance, includes one for nitrate which was also adopted by Wark (1938, 1939) ; the Rhode Island system of tests (Gilbert, 1926) involved determination of nitrate-nitrogen only ; MacGillivray *et al.* (1930) used microchemical tests for nitrate in tomato petioles. Pettinger (Pettinger, 1931 ; Pettinger and Thornton, 1934) determined nitrate in the expressed sap of maize, and Pierre and Pohlman (1933) in the exuded sap of various grasses ; Poehlman (1935) used nitrate tests on the expressed sap of soya beans, Hester (1941) on tomato stems extracted by a sodium acetate buffer solution, Nightingale (1942, 1942a) on pineapple leaf bases, Brown (1943) on a water extract of sugar beet petioles and Harrington (1944) on snap bean stems and spinach petioles ; Bray (1945) has recently described a rapid test for nitrate in plant tissue. Emmert (1935b) considered that nitrate determinations could be carried out on petioles or succulent stems, but that on other types of material, where organic compounds interfering with the nitrate test were likely to be present in greater amount, total soluble nitrogen should be determined instead. In many instances, it seems likely that nitrate determinations have been preferred because they are so easily carried out by colorimetric methods, usually involving the use of phenoldisulphonic acid.

PHOSPHORUS. Much less work than in the case of nitrogen has been done on the various chemical forms in which phosphorus and sulphur occur in the plant tissues and on the relation of the concentrations of these fractions to the nutrition of the plant. Mather (1929) studied the effect of different levels of phosphorus nutrition on the content of inorganic and organic phosphorus in several species of forage plants and cereals ; in general, the content of organic phosphorus was unaffected by phosphorus supply, except at the highest levels, while that of inorganic phosphorus increased regularly in step with the treatment. Thornton (1932) suggested that the content of inorganic phosphorus should be a more sensitive index than total phosphorus because it is in that form that plants well supplied with phosphorus accumulate the excess of absorption over utilization. Pfützer and Roth (1942) found that the effect of increased phosphorus supply on the content of phosphatide-phosphorus in spinach, rape and barley was less marked than that on the total phosphorus content—indicating that other fractions were more affected by the treatments than the phosphatide fraction. The Trinidad workers (Phillis and Mason, 1939 ; Mason and Phillis, 1943), studying cotton plants growing at different levels of phosphorus supply, found that the content of soluble phosphorus in the plants increased much more with the level of supply than that of the insoluble fractions.

Many investigators have confined their phosphorus analyses to phosphate ; this is true of most workers using sap or extracts of the material (Purdue University—see p. 42 ; Gilbert, 1926 ; Gilbert *et al.*, 1927 ; Pettinger, 1931 ; Emmert, 1932, 1936 ; Thornton, 1932 ; Thornton *et al*, 1934 ; Pierre and Pohlman, 1933 ; Carolus, 1936, 1938 ; Carolus *et al.*, 1938 ; Hester, 1941 ; Brown, 1941)—Neller (1935) shewed that almost the whole of the phosphorus in sap of sugar cane, sorghum and buckwheat was inorganic—and also applies to Chapman and his collaborators (Chapman, 1935 ; Chapman *et al.*, 1940) and to Ulrich (1944).

SULPHUR. Peterson (1914) analysed plants of rape, radish and clover which had and had not received sulphate fertilizer for volatile sulphur, sulphate, other soluble sulphur, and the insoluble

fraction of the element, and found that the treatment affected the sulphate content of all three species far more markedly than the other fractions—in fact the content of insoluble sulphur in rape and clover was hardly affected by the treatments. Shedd (1917) found that almost the whole of the increase in the sulphur content of clover and lucerne as a result of treatment with elemental sulphur was in the sulphate fraction. In the soybean, S. V. Eaton (1935) found that the content of organic sulphur in plants suffering from sulphur deficiency differed little from that of normal plants, but the sulphate content was considerably lower. Johnson *et al.* (1943) found that the effect of gypsum application on lucerne was to increase its sulphate content, while the content of reduced sulphur remained almost unchanged. Aiyar (1945) found no sulphate in rice plants suffering from sulphur deficiency.

OTHER ELEMENTS. The question of fractionation hardly arises in the same way in relation to the other nutrients, for little is known of the chemical forms in which they occur in plant tissues. Thorne and Wallace (1944) made an attempt to distinguish between ferrous and ferric iron in green and chlorotic leaves of fruit trees, and found the differences in the former in acetic acid or formic acid extract to be greater, if care was taken to exclude air.

Extraction Methods.

The more important extraction methods which have been used for routine diagnostic purposes are :—

EXPRESSED SAP. The expressed sap of the tissues studied has often been used for diagnostic purposes. Gilbert and his collaborators (Gilbert and Hardin, 1927 ; Gilbert *et al.*, 1927) proposed the analysis of sap from a wide range of crop plants for the three major nutrients for diagnostic purposes, the sap being obtained by grinding fresh material and straining through fine mesh silk (Gilbert, 1926) ; McCool and Weldon (1928) suggested a similar method, using sap extracted under a pressure of one ton, for phosphorus and potassium. Fonder (1929) investigated the calcium and magnesium content of the sap of bean plants grown on different soils, and Cook (1930) the nitrate content of the sap of cereals. Pettinger (1931 ; Pettinger and Thornton, 1934) used the composition of the sap of maize as a method of diagnosis of deficiencies of the three principal nutrients, and found the results to be closely related to the treatments the plants had received ; he also (1932) studied the effect of fertilizer treatment on the chlorine content of the sap. Halais (1933) and Craig (1934, 1934a) found that the phosphorus content of juice of sugar cane reflected the incidence of phosphorus deficiency and probable responses to phosphatic fertilizer treatment better than soil analysis ; they also reported that only where applications of phosphate fertilizer increased the yield was any increase in the phosphate content of the sap to be observed. Neller (1935) used sap analysis in investigations of the phosphorus nutrition of sorghum, buckwheat, sugarcane, maize and rape. Poehlman (1935) analysed the sap of soybeans for nitrate, phosphorus and potassium under various nutritional conditions, and concluded that it was not possible, as Pettinger had done, to fix critical levels for the nutrient percentages in the sap. Carolus (1936, 1937) on the other hand, working with potatoes, claimed to be able to lay down limiting values (see Table XII) for the five principal nutrients in the sap expressed from the stem, and found a similar technique valuable for other vegetable crops. Borden (1942, 1944), in an attempt to find a suitable index of the nitrogen nutrition of sugar cane, determined the nitrogen content of the crusher juice at different stages of growth, and found it related to the response to nitrogenous fertilizers applied at the time of sampling ; he had earlier (1936a) found that the phosphorus and potassium content of the crusher juice was related to the supply of these elements in the soil, and to the yield. In connection with work involving the analysis of expressed sap, it should be remembered that it has sometimes been reported that sap composition may be considerably affected by variations in the pressure used to obtain it (McCool and Millar, 1917 ; Knudson and Ginsberg, 1920 ; Fonder, 1929a), and even by differences in the rate of attaining the same final pressure (Gassner and Goeze, 1932), unless the material has first been killed. According to Phillis and Mason (1937), differences in composition of sap expressed from living material with varying pressure are probably to be ascribed to uncontrolled shearing strains, which are difficult to avoid in practice.

Most investigators using expressed sap do not appear to have compared the value of the

sap composition as a diagnostic index with that of the whole plant material from which it was expressed. Cook (1930) found the differences in the nitrate content of cereal sap with varying treatment much more marked than those in the total nitrogen content of the plant. Carolus (1936, 1937) also claimed to have found that the sap analyses represented the nutritional state of the plant better and shewed more marked differences than the analyses of the whole material, which he also carried out. Craig (1939a) found that the sap of sugar cane reflected differences in phosphorus nutrition much more markedly than the total phosphorus content of the leaves, but regarded the former as a less satisfactory diagnostic index because it was subject to very large varietal differences. Phillis and Mason (1940) found that the proportion of "adsorbed" (i.e., not sap-soluble) potassium in the cotton plants with which they were working increased with potassium supply, which suggests that the sap concentration would not be the most satisfactory index of nutritional status.

The results of Marsh and Shive (1941) on boron nutrition of maize indicate that, since in this plant a large proportion of the boron present can be expressed with the sap, differences in boron content of the sap are little more marked than those in total boron content; Eaton (1944) found that the proportion of the total boron in many plant species present in the expressed sap varied little under very diverse conditions of boron supply. On the other hand, Fudge's (1943) results with grapefruit indicate that, while at low boron supply levels the boron content of the sap remains almost constant in spite of an increase in the total boron present in the tissue, at toxic levels the concentration in the sap increases much more markedly than the total boron; working with squash leaves, Smith (1944) found that the boron content of sap obtained by gentle pressure decreased more markedly under boron deficiency than any other boron fraction studied.

It has been suggested (Somers and Shive, 1942) that the iron and manganese present in the sap represent the "active" fractions of these elements, but this is contested by Arnon (1943), and does not seem in accord with some of the experimental evidence mentioned below. The data of Somers and Shive in fact suggest that symptoms of manganese deficiency or toxicity are reflected more markedly in the manganese content of the press cake than in that of the sap.

Extraction by Water. Extraction with cold or hot water has frequently been used as a method of preparing diagnostic samples of plant material for analysis. Nightingale has shewn (Nightingale, 1937; Nightingale *et al.*, 1931) that in plants suffering from calcium deficiency, unlike others adequately supplied with this element, almost the whole of the calcium present is insoluble in water. Marsh (1942) found the soluble calcium content of tobacco, bean, maize and oats to vary much more widely with calcium supply than the insoluble fraction, and the same held for boron. Haas's investigations of the water-soluble and insoluble boron content of avocado leaves (1943), of the tops and roots of date palms (1944) and of citrus leaves (1945) confirm this finding. The evidence already cited supporting the determination of nitrate, phosphate or sulphate concentration rather than the total content of nitrogen, phosphorus or sulphur will also indicate the use of aqueous extracts.

Burkhart and his colleagues (Burkhart, 1941, 1942; Burkhart and Page, 1941; Collins *et al.*, 1941; Page and Burkhart, 1941; Burkhart and Collins, 1942; Lineberry *et al.*, 1944) have used extraction of the fresh material with boiling water as a diagnostic method for peanut, cotton, and strawberry, the extract being analysed for the six principal nutrients. In many of their investigations on fertilizer trials, a tolerably close relationship was found between the analytical results and the fertilizer responses observed. This technique was compared with analysis of the whole mineral content of the plant material in relation to the reduction in internal concentration of calcium and magnesium by potassium-containing fertilizers (Burkhart, 1941); this reduction was more evident in the water extract of the lower leaves than in the total content of these elements in either the leaves or the whole plant. In strawberries, on the other hand (Lineberry *et al.*, 1944), the phosphorus content of hot water extract and of whole leaf material shewed similar differences with phosphate fertilizer treatment.

Brown (1943) used water extracts of petioles for the determination of the nitrate and phosphate status of sugar beet. Brickley (1943), too, used aqueous extracts of leaves of potato and pea for potassium determinations.

With water, as with other extracting media, it is important to keep the conditions under

which extraction takes place constant. For instance, Scarseth (1943) reported that drying of plant material altered the proportion of the potassium in it which was soluble in water.

EXTRACTION BY 2% ACETIC ACID. The use of this extracting fluid for plant material appears to have been introduced by Emmert (1932, 1934, 1935). He carried out tests on the extracts for nitrate, phosphate and potassium, and used the method on many species, principally vegetable crops. Carolus, too (1938, 1938a), used 2% acetic acid as a routine method of extraction of stems and petioles for diagnostic purposes; his analyses generally included calcium and magnesium, as well as the elements studied by Emmert. Both these investigators appear to have obtained very satisfactory practical results by this technique. Hill and Johnston (1940), later adopted it in an investigation of magnesium deficiency of apples, R. L. Cook, (1941) for the study of potassium deficiency in white bean, Lorenz and Minges (1942) in work on lettuce nutrition and Ulrich (1944a) for analyses of clover petioles.

The results of Carolus (1938a) indicate that—at least as far as the metallic nutrients are concerned—the proportionate changes in their concentration in the acetic acid extract are similar to those in the whole plant material. Ulrich (1942b), however, claimed that the phosphate content of the acetic extract provided a better index of phosphorus nutrition than the total phosphorus content of the material, while the results of Lorenz (1944) showed that the differences in nutrient concentrations in the acetic acid extracts of potato petioles with nutrient supply were more marked than those in total nutrient content.

Thorne and Wallace (1944) found that more iron was extracted by acetic acid from green leaves than from others suffering from iron chlorosis.

EXTRACTION BY SODIUM ACETATE BUFFER SOLUTION. In 1935 Morgan proposed the use of a mixed acetic acid-sodium acetate solution buffered at pH 4.8 for the extraction of nutrients from both soils and plant material. This method was adopted by Walsh and other workers in Eire (Walsh, 1942; Walsh and Clarke, 1942) and applied with some success to practical problems arising in advisory work. A similar solution has been used (Davidson and Blake, 1938; Davidson, in Hambidge, 1941) for extraction of peach shoots in nutritional experiments, for apple petioles (Potter and Percival, 1938), by Wolf (1942) on stems of lima beans and by Plant *et al.* (1945) on petioles of various crop plants.

The tests described by Hester (1941) and Wolf (1943) also involved the use of an acetate buffer solution, extraction taking place in a special apparatus in which the fresh plant material was mechanically disintegrated (Hester, 1940). Greenhill (1945) found that the time of extraction with Morgan's solution was an important factor, since the rate of extraction of potassium shewed little slackening after two hours, and that of phosphorus after three hours. The phosphorus content of extracts of barley stems by this solution reflected the manurial treatment which the plants had received less well than that of normal hydrochloric acid extracts.

EXTRACTION BY HYDROCHLORIC ACID. In his method of triple analysis, Lundegårdh (1939, 1941) extracted dry leaf material for spectroscopic analysis with dilute hydrochloric acid; this technique has since been adopted by Hale (private communication). Lundegårdh (1941) claimed that the whole of the metallic elements included in the spectrographic analysis were dissolved by N hydrochloric acid; Goodall's (unpublished) determinations shewed this to be substantially true, though some 5% of the total calcium present remained in the residue. Greenhill (1945) found that extraction of fresh material with normal hydrochloric acid took at least two hours to reach completion.

Oserkowsky (1933), Thorne and Wallace (1944) and Jacobson (1945) found that the amount of iron contained in an extract of leaf material by N hydrochloric acid was related to the incidence of iron chlorosis; as already indicated, however, Somers and Shive (1942) found the difference between the amounts of iron extractable by 0.1 N and 0.5 N hydrochloric acid a better index in lime-induced chlorosis. According to Liebich (1941) the proportion of iron in spinach leaves soluble in centinormal hydrochloric acid is low under conditions of iron deficiency, which suggests that this fraction would be a better index of iron status than the less soluble portion. The methods of Plant *et al.* (1945) include the use of concentrated hydrochloric acid for the extraction of iron and zinc.

EXTRACTION BY 1% SULPHURIC ACID. Emmert (1931) used this extractant in his investigations of the phosphorus nutrition of tomato and lettuce plants grown in soils of varying acidity.

EXTRACTION BY ETHYL ALCOHOL. Beauchamp and his collaborators, in a series of investigations on the nutrition of sugar cane (Beauchamp 1939 ; 1940a ; Beauchamp and Alvarino, 1940 ; Beauchamp and Lazo, 1938 ; Beauchamp *et al.*, 1934, 1935) and potato (Beauchamp, 1940, 1942) extracted the leaves with alcohol, the extract being referred to as " crude chlorophyll." The extract was analysed for the five principal nutrients, and in samples from plots in field trials receiving different fertilizer treatments a relation was found between the treatment and the composition of the extract. In certain investigations (Beauchamp, 1940a, 1942 ; Beauchamp *et al.*, 1934) the extracted residue (" leaf skeleton ") was analysed as well as the " crude chlorophyll " ; the surprising result was obtained that while the potassium content of the extract was closely related to the potassium status of the plants as shewn by their treatment and growth, that of the " leaf skeleton " shewed no such relation. Consequently the " crude chlorophyll " was considered to provide a better index of the potassium nutrition of the plant than either the extracted residue or the whole leaf material.

The soils on which Beauchamp worked appear to have been deficient only in potassium, so there is no reason to suppose that his results apply equally to other nutrients. Though Das (1936) found that the percentage of alcohol-soluble nitrogen in the sugar cane was increased by nitrogen application more markedly than that of total nitrogen, Eaton's (1941) results with sunflower shew that the same does not apply to sulphur—in fact the alcohol-soluble fraction tended to be higher under conditions of deficiency ; similar results were obtained with black mustard (Eaton, 1942). In relation to potassium, however, Beauchamp's results are sufficiently striking to be well worth testing in other localities and on other crops.

OTHER METHODS OF EXTRACTION. In the Purdue University system of tissue tests see (p. 42) and in certain others, the reagents are added directly to the fresh plant material. This amounts to a very brief extraction with the solvent used for the reagent, which in the Purdue tests is concentrated sulphuric acid in the case of nitrate, dilute hydrochloric acid in the case of phosphate, and dilute acetic acid, sometimes with alcohol added, in the case of potassium.

Under the general heading of extraction methods, it is convenient, though perhaps not strictly accurate, to include the use of exuded sap. This seems first to have been proposed by Sabinin and his colleagues (Sabinin, 1928 ; Sabinin *et al.*, 1929) ; since in the sap collected from variously fertilized plots of oats and barley the phosphorus concentration was not closely related to the yield of the plants (although consistently related to the phosphorus fertilizer treatments they had received), the weight of phosphorus contained in the sap gathered over a certain period was considered a more reliable index. Lowry and Tabor (1931) described a method for collecting sap from the cut ends of maize stems for analytical purposes, and Lowry *et al.* (1936) later used this method in investigations on a fertilizer trial. They found that the potassium and phosphorus contents of the sap were higher with fertilizer treatments containing these elements but that the nitrogen content did not reflect the treatments. In West Virginia also (Pierre and Pohlman, 1933 ; Pohlman and Pierre, 1933) analyses of the exuded sap of maize, Sudan grass and sorghum were carried out, and it was found that the phosphorus content was related to the phosphorus status of the soil on which the plants were growing. Evans (1941) found that the composition of the exuded sap of sugar cane reflected deficiencies of potassium and phosphorus. Lundegårdh (1945) made an elaborate study of sap exuded by wheat, and shewed that its composition rapidly altered in accordance with changes in the medium in which the plants were grown.

Oserkowsky (1932) extracted the tracheal sap from branches by displacement. He was not able to find consistent differences in the iron content of the sap from chlorotic and normal branches.

A method, suggested by Spurway (1940) and called " electro-foliar diagnosis," may also find a place here. Leaves were placed between two filter papers moistened with acetic acid, and a potential difference of 45 volts maintained between these filter papers for two minutes. Some of the free ions in the leaves migrated to one or the other filter paper and could there be detected by appropriate colour reactions. This method does not seem to have achieved practical application.

It will be noted that relatively few of the proposed extraction techniques have been subjected to tests in comparison with other possible extraction methods or with analysis of the whole material. It is, of course, true that the arguments and experimental evidence cited above as supporting the use of inorganic or soluble fractions of nitrogen, phosphorus and sulphur rather than their total content or more fully elaborated fractions for diagnostic purpose will also, to some extent, support the use of many of the extraction methods in place of analysis of the whole material, since most of the extraction methods mentioned will remove preferentially the unelaborated fractions of these three elements. These arguments do not, however, apply to determinations of the other nutrient elements; but it is usually convenient to determine all the nutrient elements under study in the same solution, and the use of the same extract for all determinations can be defended on these practical grounds.

Chemical and Physico-chemical Methods of Nutrient Determination in Plant Material.

Little need be said here about the chemical methods for determining nutrient elements in whatever material is prepared for analysis. The standard chemical methods– as described, for instance, by Piper (1942a), or those of the Association of Official Agricultural Chemists (Skinner, 1935)—may always be used, though they are often inconveniently lengthy, and unnecessarily accurate considering the large errors between replicate samples of plant material. Several systems of tests specially devised for use with plant material samples have been published; among them may be mentioned those of Gilbert (1926); Emmert (1929, 1929a, 1930, 1932, 1935a, 1935b, 1942a, 1944, 1944a); the Purdue University workers (see p. 42); Morgan (1935, 1937), also intended for soil extracts; Hance (1936, 1937, 1941; Nishimura and Hance, 1938), also used for soils; Carolus (1938); Wall (1940); Parks *et al.* (1943); Wolf (1943, 1944, 1944a); Lindner and Harley (1942; Lindner, 1944); Peech and English (1944), whose tests, though primarily intended for soils, were also meant to be applicable to plant extracts, and were in fact so applied by Harrington (1944) and by Boynton and Peech (1945); and Plant *et al.* (1945).

The determination of the trace elements in plant material presents special problems because of the small quantities present; several special colorimetric methods for boron determination have been published, for instance (Berger and Truog, 1939, 1944; Maunsell, 1940). Spectrographic methods have been used fairly widely for diagnostic purposes, notably by Lundegárdh (1931, 1932, 1934, 1935, 1938, 1939, 1941, 1943) and Roach (1939a, 1940, 1943; Roach and Bolas, 1943; Roach *et al.*, 1939); others who have reported the use of spectrographic analysis for diagnostic determinations include Jones (1938); Sen (1938); Gaddum *et al.* (1939); Spencer and Lavin (1939); Keiller (1939); Shear and Ussery (1940); Goodall (1943, 1945, 1945a); and Vanselow (1945). The polarograph has been found useful for zinc determinations (Hoagland *et al.*, 1937; Lyman and Dean, 1942; Piper and Walkley, 1943; Roach and Bolas, 1944; Roach, 1945; Riches, 1945).

The neat semiquantitative method of Kidson (Kidson, 1942; Cawthron Inst., 1942, 1943; N. Z. Dep. sci. industr. Res., 1942) may be mentioned. A leaf is ashed on a porous tile, and the resulting ash skeleton is sprayed with a reagent giving a coloured product with some nutrient element in the leaf ash. Not only the intensity of the colour but also its distribution over the leaf area may be of diagnostic value.

METHOD OF EXPRESSION AND INTERPRETATION OF RESULTS.

Methods of Expression of Results of Diagnostic Analysis.

From very early in the history of agricultural chemistry it has been a convention to express chemical analyses in terms of *oxides* of most of the elements—as P_2O_5, K_2O, CaO, MgO, Fe_2O_3 Al_2O_3, SiO_2 and others. The practice (illogically) was never applied to nitrogen. A good many of the investigators whose work has been under discussion have persisted in this practice—presumably in deference to tradition, for no rational defence of it has been found. Many workers now are, however, expressing their results in terms of elements, and this is almost universal in investigations of the trace elements. The concurrent use of the two forms of expression has sometimes led to ambiguity and misunderstanding. For instance, Burkhart and Page (1941) say that their "results seem to indicate that peanuts . . . . will respond to calcium, potassium and

phosphorus if the concentrations of these soluble mineral nutrients . . . are much below 4,500, 5,500 and 600 p.p.m. respectively," whereas it is clear from the Tables to which reference is made that these concentrations relate to the oxides; if the figure of 600 p.p.m. referred to *phosphorus* strictly, none of the figures quoted would approach it, the highest being 750 p.p.m. P_2O_5. Hill (1943) also in his text mentions certain internal concentrations of " potassium," whereas corresponding figures in his tables are for K_2O. Wallace (1939), in comparing his calcium analyses of apple leaves with those of Garner *et al.* (1930), appears to have misread the latter as CaO, when in fact they were figures for Ca.* Some workers, notably Lundegårdh, have expressed their results in terms of milliequivalents; however, in the case of elements of variable valency, this involves an assumption as to the form in which they are present in the plant. The practice of expressing results in terms of the weight of the element present has been generally adopted in this paper, and results expressed in other ways have been converted in many cases. The choice between these methods of expression is however, in the main, purely a matter of personal preference and convenience.

If the necessary information is available, the weight of nutrients present in the plant material analysed may be expressed per plant, per leaf, per unit leaf area, or on a basis of fresh weight, dry weight or ash weight. Where sap or an extract has been used for analysis, the results may be reported on a volume basis.

The question of which of these methods of expression is the most appropriate in any particular case should be approached in the same way as the other methodological questions discussed above—that is, the regression should be computed of the yield increment due to fertilizer treatment on mineral content expressed in each of the possible ways, and the method of expression giving the lowest error term when the regression has been fitted should be chosen. This choice must, however, be subject to convenience.

No comparative tests of different methods of expression seem to have been carried out by this rigorous method, although data are available in the literature permitting it to be done—at least under the restriction already mentioned, that fertilizer applications have taken place before the samples were gathered. For instance, the data of McDonald and Rodriguez (1935) on cacao would permit a comparison of the dry weight and ash weight as bases for the expression of results of leaf analysis, and those of Lorenz (1942) on boron content of leaves and roots of beet could be expressed on a basis of fresh weight, dry weight or ash weight.

Results Expressed per Plant or per Leaf. For this, the number of leaves of which the sample consists, or the number of plants represented in it, must be known, together with the weight of the whole sample if only a part of it is analysed; if the whole is analysed the result will be obtained directly in this form.

Expressing results on a " per plant " basis may be quite impracticable with perennial crops, and may be very troublesome with annual crops, especially when they tiller freely; it has in fact rarely been proposed as a basis for diagnosis.

In the field, nutrient intake per unit area of ground is a form of expression almost equivalent to content per plant. Münter (1919, 1920) considered this the most suitable index of nitrogen nutrition of wheat, barley and sugar beet, since it showed most clearly the difference between control plots and those receiving a complete fertilizer; he considered that nitrogen supplies were adequate when the nitrogen uptake of barley straw was more than 9 kg/ha, or when that of sugar beet exceeded 100 kg/ha or that of the tops alone 50 kg/ha, while for wheat the sum of the nitrogen, lime and magnesia taken up should exceed 60 kg/ha in the grain and 30 kg/ha in the straw. However, if his results are recomputed on the basis recommended here it will be found that the correlation of yield increment due to nitrogenous fertilizer with these indices is small ($r = -.2827$, $r = -.4894$ using total uptake of whole plant and yield increment of beet roots or wheat grain respectively) whereas the correlation with percentage of nitrogen in the dry matter is much higher ($-.7968$, $-.4573$ with percentage in beet roots and tops, $-.7597$ and $-.6375$ with percentage in wheat grain and straw.)

* " the minimum calcium requirement of tobacco, as measured by calcium content of the upper leaves, lies between 1.1 and 1.5 per cent (1.5 to 2.1 per cent CaO) . . . . the minimum content of calcium in the leaf required to prevent deficiency symptoms is in excess of 1 per cent." (Garner *et al.*, 1930); " the amounts of the two former " (lime and magnesia) " agreeing well with the amounts stated by Garner *et al.* . . . as necessary for the healthy growth of the tobacco leaf, viz. above 1.0% CaO and 0.4% MgO." (Wallace, 1939).

Frear and Anthony (1943) computed the nitrogen content per leaf (lamina only) in apple trees receiving different amounts of nitrogenous fertilizer, and concluded that it furnished "a more consistently reliable reflection of nitrogen fertilization" than leaf size. They did not test the possibility of using percentage of nitrogen in the dry matter in the same way, but their data suggest that this would be an even better index than milligrams of nitrogen per leaf. Gossard (1943) found that the variability of nitrogen content per leaf in pecan was much greater than when expressed as a percentage of dry matter, and hence preferred the latter mode of expression. Drosdoff (1944) considered that results of leaf analysis were sometimes better expressed on a unit leaf basis. Martin (1940) used this form of expression for his nitrogen analyses of grapefruit leaves.

Results Expressed Per Unit Leaf Area. This will require measurement of leaf area in such a way as to relate it to the primary basis of expression of the results (whether per leaf, per unit fresh weight, per unit dry weight, etc.) unless the sample is obtained by some such method as the Ganong leaf punch, in which case determining the nutrient content of a given number of punch samples will give the results on an area basis directly. If this is done, however, care must be taken that diurnal changes in area of the leaf (Thoday, 1909) do not vitiate the results.

Lindner (Lindner, 1944; Lindner and Harley, 1942, 1944) considers that to express results of leaf analyses on an area basis is often preferable to the more usual dry matter basis. He points out (private communication) that if a nutrient deficiency affects carbohydrate accumulation, differences in composition expressed in these two ways may be far from identical and may even be in opposite senses—the nitrogen content of a chlorotic leaf may be high on a dry matter basis, though low on an area basis. Thorne and Wallace (1944), too, preferred to express their results for leaf composition on an area basis. The fact that, if a leaf punch is used and results expressed on an area basis, weighing the samples can be eliminated is a point of practical value (Hance, 1937; Lindner and Harley, 1942; Chem. Dept. Exp. Sta., H.S. P.A., 1944); some who use leaf punches, however, prefer to express their analytical results on a dry matter basis (Yuen and Hance, 1939; Borden, 1942, 1944).

Results Expressed on a Fresh Weight Basis. Where the fresh material or an extract of it is used for analysis, this is the most obvious basis for expressing the results. If, however, material stored in a dry state is used, an estimate of the water content of the fresh material will be needed. Expression of the results of analysis of fresh material extracts on a basis of the volume of the extract may be included under this heading since, provided the experimental procedure is not varied, such results may generally be converted to a fresh weight basis by use of a constant factor. The same applies almost as much to results of analyses of expressed sap quoted per unit volume.

Few comparisons between this and other modes of expression appear to be extant. According to the data of van Ginneken and Bruinsma (1938), the correlation of sugar yield from beets grown in different fields with the nutrient content of their foliage is slightly higher when the latter is expressed on a fresh weight basis than on a dry weight basis. Hilgeman (1941) claimed that, in grapefruit leaves, "percentage of nitrogen on a fresh weight basis . . . presents a more accurate picture of nitrogen levels than the percentage based on the dry weight." Nightingale (1942a) argued that expressing results of analyses of mature tissues on a basis of sap volume avoided the difficulties introduced by differences in the degree of lignification. Iljin (1943) also favoured expressing analytical results on a basis of cell sap.

Most of those who have analysed extracts of fresh material for diagnostic purposes have expressed their results on a fresh weight basis.

Results Expressed on a Dry Weight Basis. This is the most commonly used method of expression, the dry material being the most usual starting point for the analytical process. When the analysis (or the extraction preliminary to analysis) is performed on fresh material, the water content of this fresh material must be known if it is desired to convert the results to a dry matter basis. Thomas and Mack (1939b) considered that a dry matter basis was the only suitable one for expressing the results of diagnostic plant analysis, but did not demonstrate this; indeed, the method of expressing the primary analytical results would not affect the values of the "NPK-

Unit " on which they largely base their conclusions. (p. 41). Yuen and Hance (1939) considered that, because percentages of nutrients in sugar cane leaf samples were greater on a dry weight than on a fresh weight basis, the former mode of expression was to be preferred.

RESULTS EXPRESSED ON AN ASH BASIS. Many analytical methods involve ashing the material before making determinations for individual nutrient elements. If this is done the results may readily be expressed on an ash basis provided the ash has been weighed. In other cases, a special determination of the ash content of the material would be required. This method of expression is equivalent to determining the ratio of the nutrient element considered to other non-volatile mineral constituents.

Anderssen (1932) found that the differences between the copper content of different parts of normal fruit trees and of others suffering from copper deficiency were more obvious on an ash basis than on a dry weight basis; indeed, if a deficiency affects assimilation without affecting proportionately the intake of other ash constituents, this is to be expected—but that is not to say that the variability of results expressed on an ash basis may not be greater. Brandenburg (1932, 1939) has shewn that the boron content in the roots of beet suffering from boron deficiency is almost normal on a dry matter basis, but low as a percentage of ash (see Table I). Smith and Nash (1937) regarded variations in the percentage ash content of the dry matter of potato as an argument against expressing analytical results on a dry matter basis. On the other hand, Alway *et al.* (1926) considered that this variation in the percentage ash content, bearing no consistent relation to fertilizer treatment, was a reason for preferring to express results on a dry matter basis. The results of McDonald and Rodriguez (1935) showed that, in a fertilizer trial with cacao in which there were marked responses to potassium-containing fertilizers, the correlation of yield with potassium content of the leaves was higher when the latter was expressed on a dry matter than on an ash basis.

A number of investigators using plant analysis for diagnostic purposes have expressed their results as percentage of ash. Wallace did so in several of his investigations on the nutrition of fruit plants (Wallace, 1928, 1929b; Wallace and Mann, 1926), as did Hill and Johnston (1940) in their investigation of magnesium deficiency in the apple; Hardy and his colleagues did the same with cacao and grapefruit (Hardy, 1937; Hardy and Rodriguez, 1935; Hardy *et al.*, 1935; McDonald and Rodriguez, 1935), Follett-Smith (1934, 1939) with sugar cane, de Haan and Schoorel (1940) with tea and Chapman (1941) with rubber.

Methods of Interpretation of Results of Diagnostic Analysis

INTERPRETATION BASED ON PERCENTAGE NUTRIENT CONTENT. In interpreting the results of diagnostic analyses, it is of course essential to have standards of reference, and it is equally essential that these analytical standards should be linked with data on the performance of the plants from which they are derived. A practice which has often been adopted is to use analyses of material from a plant or site where the performance was particularly good as a standard, and to regard any deviations from this standard as being due to less satisfactory nutritional conditions, which would account for poorer performance. This is a very inadequate basis for the interpretation of diagnostic analyses, for the standard material might be well within the " luxury consumption " range for several nutrients, and hence a lower percentage of these might involve no diminution in yield and no increased probability of response to fertilizer treatment. This objection is somewhat diminished when a normal range, based on good plants from a considerable number of diverse sites, serves as a basis for comparison; but even in this case a deduction that the yield of a plant in which the percentage of one nutrient falls below the normal range would be increased by application of a fertilizer containing this nutrient can be little more than speculation, unless the data on which the normal range was based were selected from a wider range of observations covering also plants known to respond to the fertilizer in question. Until the investigator has data on the yield responses of plants at varying levels of nutrition, and on their composition, he is hardly in a position seriously to consider setting up standard values for internal nutrient concentrations.

To base the conclusions from diagnostic analyses on the data for a single element will in general be unsatisfactory. It has already been shewn that the increase in yield to be expected

from increase in the supply of a nutrient is related not only to the internal concentration of that nutrient, but also to that of other nutrients. Consequently a method of interpretation of the results of diagnostic analyses must not only take account of the value for the nutrient primarily considered, but must also allow for variations in the internal concentration of the other nutrients. This seems now to be fairly generally recognized (c.f. Emmert, 1935a; Hester, 1941; Hoffer, in Hambidge, 1941; Collins, 1942; Drosdoff, 1944), but usually only to the extent that the investigator assures himself that nutrients other than the one under investigation are not "limiting".

The ideal method of interpreting diagnostic analyses so as to allow for the effect of the internal concentration of more than one nutrient on the expected yield increase with the proposed treatment is, as has already been indicated (p. 58), by a multidimensional diagram, or an equivalent algebraic expression. So exhaustive a treatment has never been attempted; the nearest approach to it has been in the "triple analysis" method of Lundegårdh (1941, 1943), who restricted himself to determining the effect of a single level of treatment with each of the three principal fertilizer elements, and produced graphs connecting the increase in yield as a consequence of these treatments with the content of the nutrient in question in the leaves, within certain specified ranges of content of the other principal nutrients. He considered, however, that a verbal description of the yield increments to be expected with fertilizer treatment at different levels of nutrient content was the most practical way to present his conclusions, and these are summarized in Table VI.

Table VI

Probable effect of fertilizer application on grain yield of oats (from Lundegårdh, 1941)

(nutrient content of leaves in m.e. per cent. of dry matter)

		Very Good	Good	Average	Doubtful	None
Effect of 100-150 kg/ha muriate of potash (40%) in addition to 150-200 kg/ha saltpetre.						
K content — with P content	<4.5	——	10 — 20	20 — 40	40 — 50	>50
K content — with P content	4.5-6.5	<20	20 — 30	30 — 50	50 — 60	>60
K content — with P content	>6.5	<30	30 — 40	40 — 60	60 — 80	>80
Effect of 150-200 kg/ha superphosphate (20%) in addition to 150-200 kg/ha saltpetre.						
P content — with N content	<100	——	——	1 — 8	8 — 9	>9
P content — with N content	>100	4	4 — 6	6 — 8	8 — 9	>9
Effect of 150-200 kg/ha saltpetre						
N content — with P content	<4.5	——	20 — 80	80 —120	120—160	>160
N content — with P content	4.5-6.5	<100	100—120	120—200	200—250	——
N content — with P content	>6.5	<120	120—200	200—250	——	——

It should be clearly understood that the magnitude of a potential yield response will depend not only on the previous nutritional history of the plant, but also on the amount and type of fertilizer material which it is proposed to apply. The value of such data as those in Table VI is therefore somewhat limited; for though the probable increases to be expected from fertilizers containing the same element are likely to be related in a simple way depending upon their solubilities and other ascertained characteristics, on the other hand the returns for varying dosages will depend upon the form of the yield dosage relation and this, as we have seen, is dependent upon the level of other factors and therefore cannot be determined except by extensive experiments.

Among the few other workers who, in their standard values for one nutrient, have made allowance for variations in another is Emmert (1942a). He investigated the relation between the yield of tomato plants and the nitrogen content (soluble in acetic acid) of their petioles at various

stages of growth ; the plants were divided into ranges on a basis of their internal nitrogen concentration and the correlation with yield determined within each range (see also Emmert, 1937). The nitrogen value, above which such correlations tended to be negative, was regarded as optimal. The optimum could not, of course, be defined with any accuracy by this method, since its determination depended on the separation of ranges by inspection or by trial and error. Nevertheless, very interesting results were obtained, and among them was the observation that during the fruit-setting period the nitrogen optimum was lower if the soluble phosphorus content was below 200 p.p.m. (of fresh tissue) than if it was above this figure.

Hall (1905) suggested that in the roots of mangolds the need for potassic fertilizers was indicated not by the content of potassium alone, but by the sum of the contents of potassium and sodium. This fits in well with the results of van Schreven (1937) with sugar beet, which shew that not only the incidence of deficiency symptoms, but also the sugar yield in factorial experiments with varying sodium and potassium supply is highly correlated with the sum of the percentages of the two elements in the foliage (for sugar yield, in the water culture experiment $r = 0.940$, $n = 9$; in the sand culture experiment $r = 0.899$, $n = 6$) ; but Hale's (1945 and private communication) recent results indicate that, though the appearance of symptoms of potassium deficiency depends upon the internal concentration of both potassium and sodium, the relationship is not as simple as that adumbrated by Hall. It is interesting to note that Atterberg (1888a) obtained somewhat similar results with oats (see p. 14).

Many investigators have neglected the relation of yields or yield responses to fertilizer treatment to the internal concentration of nutrients other than that primarily under study, the assumption being made either tacitly or explicitly that the content of these other nutrients falls within the fairly wide range around the optimum where variations in their internal concentrations would have little effect on diagnostic conclusions. Among such investigators, some have expressed their results in the form of curves. Craig (1940), for instance, presented curves shewing the relation between the concentrations of phosphorus and potassium in sugar cane leaves and the yield response to fertilizers containing these elements ; Crowther (1937) prepared a similar curve for nitrogen in cotton leaves ; and van Itallie (1935) plotted the *percentage* increase in yield of hay with potassic fertilizers against the potash content of hay from untreated plots. The Black Rock Forest workers (Mitchell, 1939 ; Mitchell and Chandler, 1939) published curves connecting the growth of forest trees with the concentration of nitrogen in their leaves. As already mentioned (p. 57), Macy (1936) plotted both his own data and those of a number of other workers in this way.

The majority of workers, however, have merely given verbal descriptions of certain ranges or points in such curves, without attempting to draw the whole curve. Among the earliest of such investigators was Heinrich (1882), whose conclusions are embodied in Table VII.

Table VII

Probable yield of oats in relation to nutrient content of roots at maturity (% of dry matter) (From Heinrich, 1882)

	Low	*Average*	*High*
N	0.5 — 0.6	0.7 — 0.9	0.9 or more
P_2O_5	0.1 — 0.2	0.2 — 0.3	0.3 or more
K_2O	0.1 — 0.2	0.2 — 0.4	0.4 or more
CaO	0.2 — 0.3 (?)	0.3 — 0.4	0.4 or more

Remy (1903b) characterized the phosphorus status of hop plants, as indicated by the composition of mature leaves sampled at breast height during the burr stage ("*Anflug*"), as follows :

Table VIII

Phosphorus status of hops (From Remy, 1903b)

	P_2O_5 in leaves.
Phosphorus in relative excess	>0.60
Phosphorus in adequate supply	0.55 — 0.60
Phosphorus relatively deficient	0.50 — 0.55
Phosphorus seriously deficient	<0.50

Wagner (1909) and his followers related the effect of potassium-containing fertilizers to the potash content of mixed hay as shewn in Table IX; the conclusions of van Itallie (1935), to whom reference has already been made, are also included :—

Table IX.

Relation of the effect of potassium-containing fertilizers on the yield of grassland to the potash content of mixed hay.

Effect of fertilizer according to Wagner (1909)	K_2O% in hay (With 14% moisture)	Need for fertilizer (according to Wiegner (1933))	K_2O% in hay (With 14% moisture)	Effect of fertilizer according to van Itallie (1935)	K_2O% in hay (dry matter)
Soil supply adequate	2.0 or more	Unnecessary	>2.0	Yield increase unlikely	2.35
Possibility of yield increase.	1.8	Possibly advantageous	1.6—2.0	Possibility of yield increase	2.00—2.35
Probability of yield increase	1.6	Probably advantageous	1.2—1.6	Probability of yield increase.	2.00
Very great probability of yield increase.	1.4				
Certainty of yield increase.	1.2 or less	Certainly necessary	<1.2		

Borden (1936a) characterized four levels for the potassium and phosphorus content of the crusher juice of sugar cane as follows :—

Table X

Percentages of nutrients in crusher juice of sugar cane at different levels of deficiency. (From Borden, 1936a)

	% P_2O_5	% K_2O
Low	0.025	0.15
Doubtful	0.030	0.20
Medium	0.035	0.25
High	0.045	0.35

These results were obtained with the variety H.109, and Borden adds that they " may not be reliable for other cane varieties or for H.109 grown under different conditions."

Teakle and Turton (1943) gave a similar table for the copper content of leaves of subterranean clover—not in relation to the response of the clover itself to copper treatment, but to the status of other crop plants and stock in the area :—

Table XI

Copper content of leaves of subterranean clover (p.p.m. in dry matter) as indicating the copper status of the area (From Teakle and Turton, 1943).

Deficient	<3
Subnormal	3-4.5
Low normal	4.5-7.5
Normal	7.5-15
Rich	>15

All these verbal descriptions of the nutrient status of plants falling within successive ranges of nutrient content may be regarded as the equivalent of histograms representing roughly the multidimensional diagrams which we have indicated as the ideal way of expressing these relationships, with most of the dimensions omitted.

Most investigators have not attempted to specify a series of successive ranges of different nutrient status, as in Tables VI-XI, but have merely suggested certain values or ranges of nutrient content as characterizing particular parts of the hypothetical curves. Many, for instance, have specified optimal levels or ranges, or limiting values above which the nutrient supply may be regarded as adequate and no response to fertilizers may be expected. Macy's (1936) " critical percentages " fall into the latter category, Ulrich (1943) suggested that critical percentages could be found by periodical determinations on plants at two nutritional levels ; the percentages in plants at the lower supply level at the time when an effect of deficiency on growth first became apparent was taken as critical. Some early workers (von Dikow, 1891 ; Helmkampf, 1892) regarded the nutrient content as subject to a maximum (see p. 13) at which level, apparently, fertilizer effects would be negligible. Some of the early workers, too, basing themselves upon Liebig's " Law of the Minimum," considered that when the supply of a nutrient was " in minimum " its content in the plant also tended towards a minimum percentage, and the more the nutrient content exceeded this percentage, the less would responses to fertilizers containing the nutrient be ; in this connection, it is interesting to note that Chapman (1941) in his observations on the relation between growth of rubber trees and the nutrient content of their leaves, was able to estimate what appears to be a true minimum—namely, he found that extrapolation of the curve for phosphorus gave zero growth at 3% P_2O_5 in the ash.

A summary of many of these " optimal," " minimal," " normal " and " limiting " values quoted in the literature is given in Table XII.

TABLE XII.

Standard values of nutrient content proposed in the literature.

N.B.—Letters in brackets refer to Notes at end of table.

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated)	Reference
APPLE (*Pyrus malus*, etc).					
	N	———	Leaves	Growth limited when N% < 1.70	Boynton, 1942
	N	———	Leaves	"Fair chances for both good production and good colour" when N% = 1.80-2.00	Boynton, 1942
	N	July	Leaves	Optimum yield when N% > 1.85	Boynton & Burrell, 1944
	N	Midsummer	Shoot leaves	Optimum N% = 1.85-2.00	Boynton & Compton, 1945
	K	———	Leaves	Optimum growth when K% > 1.70	Batjer & Magness, 1939
	K	———	Leaves	Response to K fertilizer treatment when K% < 0.75	Boynton & Peech, 1945
	Mg	———	Leaves	Response to Mg fertilizer treatment when Mg% < 0.20	Boynton & Peech, 1945
	B	Harvest	Fruit	Deterioration in keeping quality when B% > 0.0020	Chittenden & Thomson, 1938
	Cu	———	Leaves	Cu supply inadequate when Cu% < 0.0004	Teakle, 1942
ASTRAGALUS *racemosus*					
	Se	———	Tops	Growth reduced when Se% > 0.2	Trelease & Trelease, 1938
BARLEY (*Hordeum vulgare*)					
	N	Harvest	Straw	Minimum N% (*see* p. 57) = 0.4	Macy, 1936
	N	Harvest	Straw	"Critical percentage" of N (see pp. 57, 58) = 0.8	Macy, 1936
	N	Harvest	Grain	"Critical percentage" of N (see pp. 57, 58) = 2.2	Macy, 1936
	N	Harvest	Roots	Minimum N% (*see* p. 57) = 0.63	von Dikow, 1891
	P	Harvest	Straw	Consistent response to P fertilizer treatment when P% < 0.18	Wagner, 1915
	P	Harvest	Straw	Consistently *no* response to P fertilizer treatment when P% > 0.30	Wagner, 1915
	P	Harvest	Roots	Minimum P% (*see* p. 13) = 0.057	von Dikow, 1891
	K	Harvest	Straw	K% necessary for maximum yield = 0.42	Hellriegel, 1867
	K	Harvest	Straw	K supply inadequate when K% < 0.83	Godlewski, 1901
	K	Harvest	Grain	K% necessary for maximum yield = 0.32	Hellriegel, 1867
BASSWOOD (*Tilia* spp.)					
	N	Near end of season	Leaves	Optimum N% = 3.12-3.15	Mitchell & Chandler, 1939
	N	Near end of season	Leaves	Cannot compete effectively when N% < 2.32	Mitchell & Chandler, 1939
BEECH (*Fagus grandifolia*)					
	N	Near end of season	Leaves	Optimum N% = 2.77-2.85	Mitchell & Chandler, 1939
BEET (*Beta vulgaris*) (*see also* Mangold, Sugar Beet)					
	N	———	Leaf laminae	Minimum NO_3-N% (for satisfactory growth?) = 0.05 (I,O)	R. I. agric. Exp. Sta., 1935
	N	———	Leaf laminae	Minimum NO_3-N% (for satisfactory growth?) = 0.15 (I,P)	R. I. agric. Exp. Sta., 1935
	N	———	Petioles & midribs	Minimum NO_3-N% (for satisfactory growth?) = 0.005 (I,O)	R. I. agric. Exp. Sta., 1935
	N	———	Petioles & midribs	Minimum NO_3-N% (for satisfactory growth?) = 0.03 (I,P)	R. I. agric. Exp. Sta., 1935

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).		Reference
BLACK GUM (*Nyssa sylvatica*)						
	N	Near end of season	Leaves	Optimum	$N\%_0 = 2.75\text{-}2.85$	Mitchell & Chandler, 1939
CABBAGE (*Brassica oleracea*)						
	N	———	Midribs (?)	Optimum	$NO_3\text{-}N\%_0 = 0.03$ (I)	Gilbert & Smith, 1929
CACAO (*Theobroma cacao*)						
	N	———	Young leaves	$N\%_0$ on standard good plots	= 2.35	McDonald, 1934
	P	———	Young leaves	$P\%_0$ on standard good plots	= 0.219	McDonald, 1934
	K	———	Young leaves	$K\%_0$ on standard good plots	= 2.19	McDonald, 1934
CARROT (*Daucus carota*)						
	P	Active growth period	Petioles (?)	Reduction in yield when	$P\%_0 < 0.0125$ (G)	Hill, 1943
CELERY (*Apium graveolens*)						
	N	First third of growth period	Leaf laminae	Optimum	$NO_3\text{-}N\%_0 = 0.02$ (I)	R. I. agric. Exp. Sta., 1935
	N	Last two-thirds of growth period	Leaf laminae	Optimum	$NO_3\text{-}N\%_0 = 0.03\text{-}0.04$	R. I. agric Exp. Sta., 1935
	N	First third of growth period	Petioles & midribs	Optimum	$NO_3\text{-}N\%_0 = 0.04$ (I)	R. I. agric. Exp. Sta., 1935
	N	Last two-thirds of growth period	Petioles & midribs	Optimum	$NO_3\text{-}N\%_0 = 0.06$ (I)	R. I. agric. Exp. Sta., 1935
	N	———	Stems (?)	Optimum	$NO_3\text{-}N\%_0 = 0.03$ (L)	Gilbert & Smith, 1929
CHESTNUT OAK (*Quercus montana*)						
	N	Near end of season	Leaves	Optimum	$N\%_0 = 2.72\text{-}2.80$	Mitchell & Chandler, 1939
CITRUS (*Citrus* spp.) (*see also* Grapefruit						
	K	July-Sept.	Spring-cycle leaves from fruit-bearing branches	K supply ample when	$K\%_0 > 1.0$	Chapman & Brown, 1943, 1943a; Chapman *et al.*, 1944
CLOVER (*Trifolium* sp.) (*see also* Subterranean Clover).						
	P	———	Petioles (C)	P supply inadequate when	$PO_4\text{-}P\%_0 < 0.06$	Ulrich, 1944a
	K	———	Petioles (C)	K supply inadequate when	$K\%_0 < 0.8$	Ulrich, 1944a
CORSICAN PINE (*Pinus laricio* var. *Corsicana*)						
	N	Seedling stage	Plant	Optimum	$N\%_0 = 3.0$	Gast, 1937, from data of Aldrich-Blake, ? 1930
FIELD BEAN (*Vicia faba*)						
	Mn	Harvest	Leaves	Response to Mn fertilizer treatment when	$Mn\% < 0.01$	Marsh & Powers, 1945
FLAX (*Linum usitatissimum*)						
	K	Harvest	Straw	K supply inadequate when	$K\%_0 < 0.58$	Nicholas 1945
GRAPE (*Vitis vinifera* etc)						
	N	Autumn	Leaves (of bearing vines)	No response to N fertilizer treatment when	$N\% > 1.56$	Wagner, 1907
	N	Autumn	Yellowing leaves	N supply adequate when	$N\% > 1.55$	Wagner, 1911, 1924

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).	Reference
GRAPE (*Vitis vinifera* etc.)—continued					
	P	Autumn	Leaves (of bearing vines)	No response to P fertilizer treatment when P% > 0.19	Wagner, 1907
	P	Autumn	Yellowing leaves	P supply adequate when P% > 0.20	Wagner, 1911, 1924
	K	Autumn	Leaves (of bearing vines)	No response to K fertilizer treatment when K% > 1.03	Wagner, 1907
	K	Autumn	Yellowing leaves	K supply adequate when K% > 1.04	Wagner, 1911, 1924
	Cu	———	Leaves	Cu supply inadequate when Cu% < 0.0004	Teakle, 1942
	Cu	Mid-Dec. (Q)	Leaves	Vigorous growth when Cu% = 0.00075-0.00100	Teakle *et al.*, 1943
GRAPEFRUIT (*Citrus paradisi*) [*see also* Citrus]					
	N	———	Leaves	Standard N% = 2.38	Hardy & Rodriguez, 1935; Hardy *et al.*, 1935
	N	Apr.	Leaves	Optimum N% = 2.1-2.2	Finch, 1944; Jones 1944
	N	Sept.-Nov.	Leaves	Optimum N% = 1.2	Finch, 1944; Jones 1944
	P	———	Leaves	Standard P% = 0.16	Hardy & Rodriguez, 1935; Hardy *et al.*, 1935
	K	———	Leaves	Standard K% = 1.05	Hardy & Rodriguez, 1935; Hardy *et al.*, 1935
	Ca	———	Leaves	Standard Ca% = 6.13	Hardy & Rodriguez, 1935; Hardy *et al.*, 1935
HAY (mixed) [*see also* Table IX].					
	P	———	———	P supply adequate when P% > 0.31	Hoffman, 1913; Wagner, 1909
	P	First cut	———	P supply inadequate when P% < 0.24	Liechti & Ritter, 1917
	P	Second cut	———	P supply inadequate when, P% < 0.28	Liechti & Ritter, 1917
	P	First cut	———	No P fertilizer treatment needed when P% > 0.23	Wiegner, 1933
	P	First cut	———	No response to P fertilizer treatment when P% > 0.30	van Itallie, 1935
	P	First cut	———	Response to P fertilizer treatment when P% < 0.22	van Itallie, 1935
	K	———	———	Response to K fertilizer treatment when K% < 1.66	Hoffmann, 1913
	K	———	———	Response to K fertilizer treatment when K% < 1.79-1.91	Liechti & Ritter, 1917
	Ca	———	———	Response to Ca fertilizer treatment when Ca% < 0.70	Hoffmann, 1913
HOP (*Humulus lupulus*) [*see* Table VIII]					
LETTUCE (*Lactuca sativa*)					
	N	Plants 3"-4" high	Older midribs (C)	Optimum N% = 0.15-0.20 (G)	Emmert, 1935a
	N	Plants 6"-8" high	Older midribs (C)	Optimum N% = 0.08-0.10 (G)	Emmert, 1935a
	P	Plants 3"-4" high	Older midribs (C)	Optimum P% = 0.015-0.020 (G)	Emmert, 1935a
	P	Plants 6"-8" high	Older midribs (C)	Optimum P% = 0.0100-0.0125 (G)	Emmert, 1935a
LIMA BEAN (*Phaseolus lunatus*)					
	N	Harvest	Stems (D)	Good set when N% > 0.225	Wolf, 1942
	Ca	Harvest	Stems (D)	Good set when Ca% > 0.9	Wolf, 1942
	Ca	Harvest	Stems (D)	Poor set when Ca% < 0.6	Wolf, 1942

Plant	Element	Time or stage of development	Part of plant.	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).		Reference.
LUCERNE (*Medicago sativa*)						
	K	———	Tops	Yield decreased when	$K\% < 1.0$	Hunter *et al.*, 1943; Bear & Prince, 1945
	Ca	———	Tops	Yield decreased when	$Ca\% > 2.0$	Hunter *et al.*, 1943
	S	———	Tops	"Critical percentage" of (see pp. 57, 58)	$S = 0.2$	Macy, 1936, quoting Alway, 1927
	B	Late summer	———	Normal when	$B\% > 0.0020$	Dregne & Powers, 1942
MAIZE (*Zea mays*)						
	N	Late summer	Lower stem (A)	N supply adequate when	$NO_3\text{-}N\% = 0.0200$ (I)	Pettinger, 1931
	N	———	———	Response to N fertilizer treatment probable when	$N\% < 0.70$	Macy, 1936, quoting Fraps, 1912
	P	Late summer	Lower stem (A)	Good yields when	$P\% > 0.0087$ (I)	Pettinger, 1931
	P	Late summer	Lower stem (A)	P supply inadequate when	$P\% < 0.0044$ (I)	Pettinger, 1931
	K	Late summer	Lower stem (A)	K supply inadequate when	$K\% < 0.083$ (I)	Pettinger, 1931
	K	Late summer	Lower stem (A)	K supply ample when	$K\% > 0.166$ (I)	Pettinger, 1931
MANGOLD (*Beta vulgaris*) [*see also* Beet]						
	P	Harvest	Root	Consistent response to P fertilizer treatment when	$P\% < 0.15$	Wagner, 1915
	B	Harvest	Leaves	Response to B fertilizer treatment when	$B\% < 0.0030$	Brandenburg, 1939
OATS (*Avena sativa*) [*see also* Tables VI & VII]						
	N	Harvest	Straw	Minimum N% (see p. 14)	= 0.25	Atterberg, 1888, 1889
	N	Harvest	Straw	No increase in yield with increase in N% above	1.0-1.1	Pfeiffer *et al.*, 1912
	N	Harvest	Grain	Minimum N% (see p. 14)	= 1.20	Atterberg, 1901
	N	Harvest	Grain	No increase in yield with increase in N% above	2.2-2.3	Pfeiffer *et al.*, 1912
	N	Milk-ripe	Tops	N supply adequate when	$N\% = 1.10$	Liebscher *et al.*, 1898
	N	Flowering	Tops	Minimum N% (see p. 14)	= 0.68	Atterberg, 1901
	N	Milk-ripe	Tops	Minimum N% (see p. 17)	= 0.759	Pfeiffer *et al.*, 1915
	N	Milk-ripe	Tops	"Critical percentage" of N (see pp. 57, 58)	= 1.0	Macy, 1936; quoting Pfeiffer *et al.*, 1919
	N	Harvest	Roots	Minimum N% (see p. 13)	= 0.5-0.6	Heinrich, 1882
	N	Harvest	Plant (?)	Good average development when	$N\% = 1.0$	Wolff, 1876, 1877
	N	Harvest	Plant (?)	Minimum N% (see p. 12)	= 0.6-0.7	Wolff, 1876, 1877
	N	Harvest	Plant (?)	Minimum N% (see p. 14)	= 0.80	Atterberg, 1901
	P	Flowering	Leaves	Normal range of	$P\% = 0.23\text{-}0.31$	Lundegårdh, 1938
	P	Flowering	Leaves	Growth retarded when	$P\% < 0.23$	Lundegårdh, 1938
	P	Flowering	Leaves	Normal range of	$P\% = 0.155\text{-}0.310$	Lundegårdh, 1939
	P	Harvest	Straw	Consistent response to P fertilizer treatment when	$P\% < 0.085$	Wagner, 1915
	P	Harvest	Straw	Consistently no response to P fertilizer treatment when	$P\% > 0.184$	Wagner, 1915
	P	Harvest	Grain	P supply inadequate when	$P\% = 0.26\text{-}0.31$ (E)	Atterberg, 1888a
	P	Harvest	Grain	P supply adequate when	$P\% = 0.39\text{-}0.43$ (E)	Atterberg, 1888a
	P	Harvest	Grain	Minimum P% (see p. 14)	= 0.16	Atterberg, 1901
	P	Milk-ripe	Tops	P supply adequate when	$P\% > 0.15$	Liebscher *et al.*, 1898
	P	Flowering	Tops	Minimum P% (see p. 14)	= 0.06	Atterberg, 1901
	P	Milk-ripe	Tops	Minimum P% (see p. 17)	= 0.19	Pfeiffer *et al.*, 1915
	P	Harvest	Roots	Minimum P% (see p. 13)	= 0.03-0.04	Heinrich, 1882
	P	Harvest	Plant (?)	Good average development when	$P\% = 0.22$	Wolff, 1876, 1877
	P	Harvest	Plant (?)	Minimum P% (see p. 12)	= 0.15	Wolff, 1876, 1877

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).	Reference
OATS (*Avena sativa*) [*see also* Tables VI & VII]—continued					
	P	Harvest	Plant	Yield decreased when P% < 0.13	Petersen, 1876
	P	Harvest	Plant	Minimum P% (see p. 14) = 0.09	Atterberg, 1901
	K	Flowering	Leaves	Normal range of K% = 0.78-1.56	Lundegårdh, 1938
	K	Flowering	Leaves	Normal range of K% = 0.39-1.56	Lundegårdh, 1939
	K	Harvest	Straw	K supply inadequate when K% < 0.83 (F)	Atterberg, 1888a
	K	Harvest	Straw	Minimum K% (see p. 14) = 0.23	Atterberg, 1901
	K	Harvest	Straw	Response to K fertilizer treatment when K% < 0.83	Hoffmann, 1917
	K	Milk-ripe	Tops	K supply adequate when K% = 1.15-1.27 (N)	Liebscher *et al.*, 1898
	K	Flowering	Tops	Minimum K% (see p. 14) = 0.31	Atterberg, 1901
	K	Harvest	Roots	Minimum K% (see p. 13) = 0.07-0.08	Heinrich, 1882
	K	Harvest	Plant (?)	Good average development when K% = 0.66	Wolff, 1876, 1877
	K	Harvest	Plant (?)	Minimum K% (see p. 12) = 0.42	Wolff, 1876, 1877
	K	Harvest	Plant (?)	Minimum K% (see p. 14) = 0.31	Atterberg, 1901
	Ca	Flowering	Leaves	Optimum Ca% = 0.176	Lundegårdh, 1934, 1935
	Ca	Flowering	Leaves	Retarding effect when Ca% > 0.9	Lundegårdh, 1935
	Ca	Flowering	Leaves	Normal range of Ca% = 0.72-1.0	Lundegårdh, 1938
	Ca	Flowering	Leaves	Normal range of Ca% = 0.176-1.0	Lundegårdh, 1939
	Ca	Harvest	Straw	Minimum Ca% (see p. 14) = 0.10	Atterberg, 1901
	Ca	Harvest	Tops	Minimum Ca% necessary for good development = 0.21	Wolff, 1868
	Ca	Flowering	Tops	Minimum Ca% (see p. 14) = 0.07	Atterberg, 1901
	Ca	Harvest	Plant (?)	Good average development when Ca% = 0.18	Wolff, 1876, 1877
	Ca	Harvest	Plant (?)	Minimum Ca% (see p. 12) = 0.11	Wolff, 1876, 1877
	Ca	Harvest	Plant (?)	Minimum Ca% (see p. 14) = 0.06	Atterberg, 1901
	Mg	Flowering	Leaves	Normal Mg% = 0.24	Lundegårdh, 1938
	Mg	Harvest	Straw	Minimum Mg% (see p. 14) = 0.05	Atterberg, 1901
	Mg	Flowering	Tops	Minimum Mg% (see p. 14) = 0.05	Atterberg, 1901
	Mg	Harvest	Plant (?)	Good average development when Mg% = 0.12	Wolff, 1876, 1877
	Mg	Harvest	Plant (?)	Minimum Mg% (see p. 12) = 0.06	Wolff, 1876, 1877
	Mg	Harvest	Plant (?)	Minimum Mg% (see p. 14) = 0.06	Atterberg, 1901
	S	Harvest	Straw	Minimum S% (see p. 14) = 0.06	Atterberg, 1901
	S	Harvest	Plant (?)	Good average development when S% = 0.08	Wolff, 1876, 1877
	S	Harvest	Plant (?)	Minimum S% (see p. 12) = 0.04	Wolff, 1876, 1877
	S	Harvest	Plant (?)	Minimum S% (see p. 14) = 0.10	Atterberg, 1901
	Cu	6-9 weeks	Leaves	Cu supply highly inadequate when Cu% < 0.0003	Teakle, 1942
	Cu	6-9 weeks	Leaves	Cu supply adequate when Cu% = 0.0007-0.0012	Teakle, 1942
	Zn	6-8 weeks	Plant (?)	Zn supply normal when Zn% = 0.0020	Teakle & Turton, 1943
PEA (*Pisum sativum*)					
	K	Flowering	Main stems (C?)	Optimum K% = 0.415-0.581(G)	Hill, 1943
PEACH (*Prunus persica*)					
	P	Midsummer	Leaves	Growth affected when P% < 0.11	Lilleland & Brown, 1942, from data of Cullinan *et al.*, 1939
	K	June-July	Leaves	No response to K fertilizer treatment when K% > 1.5	McCollam, 1943
PEANUT (*Arachis hypogaea*)					
	P	Early part of growing season	Lower leaf blades (B)	Response to P fertilizer treatment when P% < 0.0262 (G)	Burkhart & Page, 1941
	K	Early part of growing season	Lower leaf blades (B)	Response to K fertilizer treatment when K% < 0.46(G)	Burkhart & Page, 1941

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).	Reference
PEANUT (*Arachis hypogaea*)—continued					
	Ca	Early part of growing season	Lower leaf blades (B)	Response to Ca fertilizer treatment when Ca% < 0.32(G)	Burkhart & Page, 1941
PEAR (*Pyrus communis*)					
	Cu	———	Leaves	Cu supply inadequate when Cu% < 0.0004	Teakle, 1942
PECAN (*Carya pecan*)					
	P	Early June	Mature leaflets	Response to P fertilizer treatment when P% < 0.150	Alben & Hammar, 1940
PIGNUT HICKORY (*Hicoria glabra*)					
	N	Near end of season	Leaves	Optimum N% = 2.37-2.42	Mitchell & Chandler, 1939
PINEAPPLE (*Ananas sativus*)					
	N	14 months before flower-bud appearance	Leaf bases	N supply adequate when NO_3-N% = 0.0283 (GHR)	Nightingale, 1942, 1942a
	N	4-10 months before flower-bud appearance	Leaf bases	N supply adequate when NO_3-N% = 0.104 (GHR)	Nightingale, 1942, 1942a
	P	Early vegetative stages	Leaf bases	P supply adequate when P% = 0.020 (G)	Nightingale, 1942a
	P	Blossom-bud differentiation	Leaf bases	P supply adequate when P% = 0.028 (G)	Nightingale, 1942a
	K	———	Leaf bases	K supply adequate when K% = 0.38 (G)	Nightingale, 1942a
PLUM (*Prunus domestica*)					
	K	———	Leaves	Normal minimum range of K% = 1.5-2.0	Boynton, 1942
POTATO (*Solanum tuberosum*)					
	N	1 month after emergence	2nd or 3rd petioles from apex	Yield depressed when NO_3-N% < 0.08 (G)	Lorenz, 1944
	N	———	Lower stems (C)	Optimum N% > 0.1 (G)	Emmert, 1936
	N	———	Lower stems (A)	N supply inadequate when N% < 0.07-0.08 (F)	Carolus, 1937
	P	Tuberization	Lower stems (C)	Optimum PO_4-P% > 0.02 (G)	Emmert, 1936
	P	Beginning of season	Lower stems (A)	P supply inadequate when P% < 0.015 (I)	Carolus, 1937
	P	End of season	Lower stems (A)	P supply inadequate when P% < 0.006 (I)	Carolus, 1937
	P	Harvest	Tubers	Consistent response to P fertilizer treatment when P% < 0.17	Wagner, 1915
	P	Harvest	Tubers	P supply inadequate when P% < 0.178	Chaminade, 1942
	K	Beginning of season	Lower stems (A)	K supply inadequate when K% < 0.18 (I)	Carolus, 1937
	K	End of season	Lower stems (A)	K supply inadequate when K% < 0.37 (I)	Carolus, 1937
	K	———	Lower stems (A)	Response to K fertilizer treatment when K% < 0.29 (G)	Carolus, 1938
	K	Harvest	Tubers	Consistent response to K fertilizer treatment when K% < 1.49	Wagner, 1915
	K	Harvest	Tubers	Consistently no response to K fertilizer treatment when K% > 2.49	Wagner, 1915
	K	Harvest	Tubers	K supply inadequate when K% < 2.38	Chaminade, 1942

Plant	Element	Time or stage of development	Part of plant.	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).	Reference.
POTATO (*Solanum tuberosum*)—continued					
	Ca	Beginning of season	Lower stems (A)	Ca supply inadequate when $Ca\%<0.043$ (I)	Carolus, 1937
	Ca	End of season	Lower stems (A)	Ca supply inadequate when $Ca\%<0.10$ (I)	Carolus, 1937
	Mg	Beginning of season	Lower stems (A)	Mg supply inadequate when $Mg\%<0.0166$ (I)	Carolus, 1937
	Mg	End of season	Lower stems (A)	Mg supply inadequate when $Mg\%<0.048$ (I)	Carolus, 1937
	Mg	Harvest	Tubers	Mg supply adequate when $Mg\%>0.101$	Chaminade, 1942
RED MAPLE (*Acer rubrum*)					
	N	Near end of season	Leaves	Optimum $N\%=2.55$-2.68	Mitchell & Chandler, 1939
RED OAK (*Quercus borealis*)					
	N	Near end of season	Leaves	Optimum $N\%=2.46$-2.57	Mitchell & Chandler, 1939
RYE (*Secale cereale*)					
	P	Harvest	Straw	Consistent response to P fertilizer treatment when $P\%<0.06$	Wagner, 1915
	P	Harvest	Straw	Consistently *no* response to P fertilizer treatment when $P\%>0.12$	Wagner, 1915
	K	Harvest	Straw	Consistent response to K fertilizer treatment when $K\%<0.66$	Wagner, 1915
	K	Harvest	Straw	Consistently *no* response to K fertilizer treatment when $K\%>0.95$	Wagner, 1915
SCOTS PINE (*Pinus sylvestris*)					
	N	Seedling stage	Plant	Optimum $N\%=3.0$	Gast, 1937
SOY BEAN (*Glycine soja*)					
	B	Harvest	Plant (?)	Reduction in yield when $B\%<0.0030$	Muhr, 1941
SUBTERRANEAN CLOVER (*Trifolium subterraneum*) [*see also* Table XI; and Clover					
	Cu	Flowering	Leaves	Cu supply inadequate when $Cu\%<0.0003$	Teakle, 1942
	Cu	Flowering	Leaves	Cu supply adequate when $Cu\%=0.0007$-0.0012	Teakle, 1942
	Zn	Flowering	Leaves	Zn supply inadequate when $Zn\%<0.0015$	Teakle & Turton, 1943
SUGAR BEET (*Beta vulgaris*)			[*see also* Beet		
	N	———	Petioles of younger mature leaves	N supply inadequate when $NO_3\text{-}N\%<0.1$	Ulrich, 1944
	P	———	Petioles of younger mature leaves	P supply inadequate when $PO_4\text{-}P\%<0.1$	Ulrich, 1944
	P	Harvest	Tops	P supply inadequate when $P\%<0.17$	Münter, 1920
	P	Harvest	Roots	Consistent response to P fertilizer treatment when $P\%<0.13$	Wagner, 1915
	K	———	Petioles of younger mature leaves	K supply inadequate when $K\%<2.0$	Ulrich, 1944
	K	Early harvest	Tops	K supply inadequate when $K\%<0.274$ (F, G)	van Ginneken & Bruinsma, 1938
	K	Harvest	Roots	Consistent response to K fertilizer treatment when $K\%<0.66$	Wagner, 1915
	B	Harvest	Leaves	Response to B fertilizer treatment when $B\%<0.0030$	Brandenburg, 1939
	Mn	Harvest	Leaves	Response to Mn fertilizer treatment when $Mn\%<0.01$	Marsh & Powers, 1945

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).		Reference
SUGAR CANE (*Saccharum officinarum*) [*see also* Table X]						
	N	6—8 months	Punch samples from centre of laminae of 2nd-4th leaves from apex	Optimum	N%=2.0	Yuen & Hance, 1939 : Doi, 1944
	N	12-14 months	Punch samples from centre of laminae of 2nd-4th leaves from apex	Optimum	N%=1.5	Yuen & Hance, 1939
	N	15-17 months	Punch samples from centre of laminae of 2nd-4th leaves from apex	Optimum	N%=1.25	Yuen & Hance, 1939
	N	24 months	Punch samples from centre of laminae of 2nd-4th leaves from apex	Optimum	N%=1.1	Yuen & Hance, 1939
	N	———	Punch samples from centre of laminae of 2nd-4th leaves from apex	Growth diminished when	N%<1.3(S)	Yuen & Hance, 1939
	N	———	Punch samples from centre of laminae of 2nd-4th leaves from apex	Growth diminished when	N%<1.0(T)	Yuen & Hance, 1939
	N	Feb.-April (Q)	Blade of 3rd leaf from apex	Optimum	N%=1.38	Craig, 1941
	N	———	Leaf blades from elongating cane	N% adequate for maximum yield	=1.0 (H)	Clements & Kubota, 1943
	N	Jan.-Apr. (Q) (5-6 months)	Blade of 3rd leaf from apex	Optimum	N%=1.35-1.45 (M)	Craig & Halais, 1944
	N	First 5-6 months	Blades of 3rd-6th leaves from apex	Optimum	N%=1.80-2.00	Clements *et al.*, 1945
	N	Middle of growth period	Blades of 3rd-6th leaves from apex	Optimum	N%=1.60	Clements *et al.*, 1945
	N	Harvest	Blades of 3rd-6th leaves from apex	Optimum	N%=1.25-1.35	Clements *et al.*, 1945
	P	———	Blade of 3rd leaf from apex	Response to P fertilizer treatment when	P%<0.13	Craig, 1940
	P	Feb.-Apr. (Q)	Blade of 3rd leaf from apex	Optimum	P%=0.16	Craig, 1941

Plant	Element	Time or stage of development	Part of plant	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).	Reference
SUGAR CANE (*Saccharum officinarum*) [*see also* Table X]—continued					
	P	Jan.-Apr. (Q) (5-6 months)	Blade of 3rd leaf from apex	Optimum $P\%=0.16$-0.18 (M)	Craig & Halais, 1944
	P	———	Leaf sheaths from elongating cane	$P\%$ adequate for maximum yield $=0.08$ (J)	Clements & Kubota, 1943; Clements *et al.*, 1945
	P	Harvest	Stems (A)	Reduction in yield when $P\%<0.017$ (I)	Borden, 1936a
	K	———	3rd leaf from apex	Response to K fertilizer treatment when $K\%<1.25$	Craig, 1940
	K	Feb.-Apr. (Q)	3rd leaf from apex	Optimum $K\%=1.81$	Craig, 1941
	K	———	Sheaths of elongating cane	$K\%$ adequate for maximum yield $=2.25$ (J)	Clements & Kubota, 1943; Clements *et al.*, 1945
	K	Jan.-Apr. (Q) (5-6 months)	Blade of 3rd leaf from apex	Optimum $K\%=1.83$-2.08 (M)	Craig & Halais, 1944
	K	Harvest	Stems (A)	K supply inadequate when $K\%<0.20$ (I)	Holmes, 1939
SUGAR MAPLE (*Acer saccharum*)					
	N	Near end of season	Leaves	Optimum $N\%=2.77$-2.85	Mitchell & Chandler, 1939
TOMATO (*Lycopersicum esculentum*)					
	N	Plant 12" high	Mature petioles (C)	Optimum NO_3-$N\%=0.10$-0.15 (G)	Emmert, 1935a
	N	During fruit set	Mature petioles (C)	Optimum NO_3-$N\%=0.07$-0.08 (G)	Emmert, 1935a
	N	Ripening	Mature petioles (C)	Optimum NO_3-$N\%=0.030$-0.035 (G)	Emmert, 1935a
	N	Before fruit set	Mature petioles (C)	Optimum $N\%=0.15$-0.20 (G)	Emmert, 1941
	N	Between setting of 1st & 4th trusses	Mature petioles (C)	Optimum $N\%=0.10$ (G)	Emmert, 1941
	N	From 4th truss to final ripening	Mature petioles (C)	Optimum $N\%=0.20$-0.25 (G)	Emmert, 1941
	N	Final ripening	Mature petioles (C)	Optimum $N\%=0.10$ (G)	Emmert, 1941
	N	Before fruit set	Mature petioles (C)	Optimum $N\%=0.15$ (G)	Emmert, 1942a
	N	During fruit set	Mature petioles (C)	Optimum $N\%=0.05$-0.08 (GK)	Emmert, 1942a
	N	During fruit set	Mature petioles (C)	Optimum $N\%=0.08$-0.15 (GL)	Emmert, 1942a
	N	Ripening	Mature petioles (C)	Optimum $N\%=0.05$-0.10 (G)	Emmert, 1942a
	N	———	Stems (D)	Healthy when NO_3-$N\%=0.008$-0.249 (G)	Hester, 1941
	P	Plant 12" high	Mature petioles (C)	Optimum PO_4-$P\%=0.02$-0.03 (G)	Emmert, 1935a
	P	During fruit set	Mature petioles (C)	Optimum PO_4-$P\%=0.035$-0.040 (G)	Emmert, 1935a
	P	Ripening	Mature petioles (C)	Optimum PO_4-$P\%=0.030$-0.035 (G)	Emmert, 1935a
	P	Before fruit set	Mature petioles (C)	Optimum $P\%=0.010$-0.015 (G)	Emmert, 1941
	P	During fruit set	Mature petioles (C)	Optimum $P\%>0.020$ (G)	Emmert, 1941
	P	Before fruit set	Mature petioles (C)	Optimum $P\%>0.02$ (G)	Emmert, 1942a

Plant	Element	Time or stage of development	Part of plant.	Performance of plant as related to percentage of element (in dry matter, unless otherwise stated).	Reference.
TOMATO (*Lycopersicum esculentum*)—continued					
	P	During fruit set	Mature petioles (C)	Optimum P% > 0.04 (G)	Emmert, 1942a
	P	———	Stems (D)	Healthy when P^{o}_{o} = 0.0043-0.0086 (G)	Hester, 1941
	K	———	Stems (D)	Optimum K^{o}_{o} = 0.166-0.249 (G)	Hester, 1941
	K	———	Plant (?)	"Critical percentage" (see pp. 57, 58) of K = 0.9	Macy, 1936; data from Hoagland & Martin, 1933
	Mg	Mid-season	Leaves from mid-stem region	Mg supply inadequate when Mg^{o}_{o} < 0.30	Jones *et al.*, 1945
TREMBLING ASPEN (*Populus tremuloides*)					
	N	Near end of season	Leaves	Optimum N^{o}_{o} = 2.64-2.77	Mitchell & Chandler, 1939
WHEAT (*Triticum vulgare*)					
	P	Harvest	Straw	Consistent response to P fertilizer treatment when P^{o}_{o} < 0.07	Wagner, 1915
	P	Harvest	Straw	P supply adequate when P^{o}_{o} > 0.065	Jakuškin, 1915
	P	Harvest	Straw	P supply almost certainly inadequate when P^{o}_{o} < 0.03-0.04	Jakuškin, 1915
	K	Harvest	Straw	Consistent response to K fertilizer treatment when K^{o}_{o} < 0.56	Wagner, 1915
	K	Harvest	Straw	Response to K fertilizer treatment when K^{o}_{o} < 0.83	Hoffmann, 1917
	Cu	6-8 weeks	Leaves	Cu supply highly inadequate when Cu% < 0.0003	Teakle, 1942
	Cu	6-8 weeks	Leaves	Cu supply adequate when Cu^{o}_{o} = 0.0007-0.0012	Teakle, 1942
WHITE ASH (*Fraxinus americana*)					
	N	Near end of season	Leaves	Optimum N^{o}_{o} = 2.80-2.86	Mitchell & Chandler, 1939
	N	Near end of season	Leaves	Cannot compete effectively when N^{o}_{o} < 2.01	Mitchell & Chandler, 1939
WHITE OAK (*Quercus alba*)					
	N	Near end of season	Leaves	Optimum N^{o}_{o} = 2.72-2.80	Mitchell & Chandler, 1939
WHITE PINE (*Pinus strobus*)					
	N	Seedling stage	Plant	Optimum N^{o}_{o} = 3.0	Gast, 1937
YELLOW POPLAR (*Liriodendron tulipifera*)					
	N	Near end of season	Leaves	Optimum N^{o}_{o} = 2.97-3.02	Mitchell & Chandler, 1939
	N	Near end of season	Leaves	Cannot compete effectively when N^{o}_{o} < 2.15	Mitchell & Chandler, 1939

TABLE XII NOTES.

N.B.—Notes A–D refer to column 4, E–P and R–T to column 5 and Note Q to column 3.

(A) Expressed sap.
(B) Hot water extract.
(C) 2% acetic acid extract.
(D) Acetate buffer extract.
(E) If ratio N/P_2O_5 > 2.
(F) With high Na supply.
(G) % of fresh material.
(H) Read from graph.
(I) % in sap.
(J) On basis of sugar-free dry weight
(K) If P content (in the same terms) < 0.02
(L) If P content (in the same terms) > 0.02
(M) Varieties BH 10/12 and Big Tanna.
(N) If N % > 1.12-1.24
(O) Under long-day conditions.
(P) Under short-day conditions.
(Q) In Southern Hemisphere.
(R) With high carbohydrate content.
(S) With unfavourable weather conditions.
(T) With favourable weather conditions.

INTERPRETATION BASED ON NUTRIENT RATIOS.—Many investigators have not regarded the content of nutrient in the plant material as a suitable index on which to base diagnoses of nutritional status, but have preferred to compute the ratios of certain nutrients within the plant for diagnostic purposes. This procedure involves certain hidden assumptions about the form of the curves relating plant development to nutrient content. Let us suppose a three-dimensional figure in which the vertical axis represented whatever feature of development was being measured (say, the response to a particular fertilizer application) while the two horizontal axes represented the content of the two nutrients in question in the plant material, all other factors being held constant; if development of the plant depends on the ratio of the two nutrients within it, and not on their individual values, then any vertical plane through the origin must cut the figure in a horizontal line. This has never been demonstrated. Gregory, in fact, was able in his experiments with barley to shew that when the supply of nitrogen and phosphorus increased in proportion ('balanced' series) the ratio of these two elements within the plant remained constant (range of mean ratios N/P_2O_5 in the whole plant up to the fifth harvest 3.35–3.80) although their concentrations individually increased, and yields rose (see Table III). Moreover, where luxury consumption occurs it is clear that an increase in the supply of the nutrient in excess may increase the ratio of its internal concentration to that of the "limiting" nutrient without affecting either the internal concentration of the latter or the yield.

It is not to be denied that the ratios of nutrients within the plant may sometimes give useful indications as a supplement to those derived from the actual concentrations—though no information that could not be obtained from a curvilinear multiple regression—, but to use such ratios without consideration of the individual concentration data is, in most cases, unjustified (c.f. Richards, 1944).

Most investigators who have proposed ratios between nutrients as criteria for diagnostic purposes have made no attempt to justify their use as against percentages of the individual nutrients—and their data often shew that the latter are at least as good an index as the proposed ratio. Münter (1919), for instance, stated that wheat was deficient in nitrogen if the $\frac{P_2O_5}{N}$ ratio in the straw was greater than 0.6, but his figures shew that the correlation of yield increment due to nitrogen-containing fertilizer with this ratio was only +0.2969, while that with the percentage nitrogen content of the straw was −0.6375. Beauchamp and Lazo (1938) considered the ratio $\frac{K_2O}{N + P_2O_5}$ in the alcohol extract of sugar cane leaves to be a better index of the performance of the cane in the field under varying conditions of potassium nutrition than the content of potash alone; if correlations are worked out between the yield increments with potassium-containing fertilizers and the values of these two indices, his data shew that while the correlation with the ratio is rather higher (the coefficients are −0.4521 and −0.4150 respectively), the difference is very small and both correlations are in any case non-significant owing to the small number of plots studied. Richards (1944) pointed out that the results of Hunter *et al.* (1943) on the calcium and potassium nutrition of lucerne are explained quite as well on the basis of the percentages of these two cations individually in the plant as by their ratio.

Lundegårdh (1934, 1935, 1939) claimed to have found that the ratio of potassium to calcium in oat leaves should lie between 1.5 and 5.0 for healthy development; values outside these limits predisposed the plant to the development of grey speck disease, also associated with manganese deficiency. Samuel and Piper (1929) had concluded that manganese deficiency alone was responsible, the limiting value being 14 p.p.m. manganese in the plant dry matter (see Table II); this Lundegårdh (1931, 1932) could not accept, since some of his oat plants in solution culture remained healthy, though containing less than 1 p.p.m. manganese (see also data in Table I). That manganese deficiency was in some way connected with the disorder he could not deny, since affected plants generally contained less manganese than healthy plants from the same field; but he also observed a correlation (though far from perfect) with the ratio mentioned. There would appear to be here a *prima facie* case for the diagnostic importance of a nutrient ratio, but further investigation is needed.

Stanford and his collaborators (1942) investigated potassium deficiency in maize, and computed the ratio $\frac{Ca + Mg}{K}$ within the plant (nutrient content being expressed as equivalents) as a diagnostic index They stated that all plants in which the ratio was less than 3.5 were normal, while those in which it exceeded 5.0 shewed more or less severe potash deficiency symptoms. Their paper does not make it too clear which of the plants studied were shewing symptoms, but, if in their Table II it is taken that all the plants from "unproductive" or "high lime" soil were shewing symptoms while the others were not, the ranges of potassium content are respectively 0.88—1.37 and 1.99—4.54 % in the dry matter, while the corresponding ranges for the ratios are 3.87—8.18 and 0.64—2.33—hardly a striking demonstration of the superiority of the latter as a diagnostic index.

Boresch (1938) investigated chloride injury of red currants—which was not always clearly distinguishable from potassium deficiency. He found no close relationship between the incidence of chloride injury and the chlorine content of the leaves—healthy leaves, for instance, might have as much as 1.9%, and affected leaves 1.4% or less—but there was a close relationship with the ratio of potassium to chlorine in the leaves, all injured leaves having values less than unity (content expressed in terms of equivalents) and all healthy leaves higher values. This did not include true potassium deficiency, symptoms of which appeared when the potassium content itself fell below a certain limiting value (see Table II), and was independent of the chlorine content. These results of Boresch on chlorine injury seem to provide an authentic instance of a nutrient ratio being of diagnostic importance.

Somers and Shive (1942) claimed to have shewn that the incidence of symptoms of iron or manganese deficiency in soybeans grown in solution culture was due solely to the ratio of these elements within the plant and thus that these symptoms could equally well be regarded as due to excess of the other element. But their figures indicate that the content of manganese alone is at least as good an index of the incidence of symptoms as the ratio of iron to manganese, as shewn in the table below :—

Table XIII

Relation of manganese deficiency and toxicity symptoms in soybean to composition of leaves and roots (from Somers and Shive, 1942).

	Symptoms of manganese deficiency (or excess iron)	Normal	Symptoms of excess manganese* (or iron deficiency)
Ratio $\frac{\text{soluble† iron}}{\text{soluble† manganese}}$ in leaves	4.47— 9.88	1.50— 2.65	0.58— 1.00
p.p.m. soluble† manganese in leaf dry matter	9.2 —10.8	15.5 — 28.6	36.3 — 83.6
p.p.m. insoluble† manganese in leaf dry matter	1.7 — 2.6	13.6 —102.4	173.4 —999.0
Ratio $\frac{\text{soluble† iron}}{\text{soluble† manganese}}$ in roots	12.4 —17.4	2.24— 5.04	1.17— 1.77
p.p.m. soluble† manganese in root dry matter	17.3 18.9	24.3 — 43.1	48.8 —149.6
p.p.m. insoluble† manganese in root dry matter	0	0 — 49.4	61.6 —168.1

*Excluding one culture (No. 3), which shewed slight symptoms of manganese toxicity, although the composition fell within the normal range consistently on every criterion used.

†By "soluble" and "insoluble" are meant the fractions of the elements found in the expressed sap and in the press cake.

The data of Kriel (1941), quoted by Bennett (1945), indicate that in tomato chlorosis is not related, within a wide range, to the manganese content of the leaves ; nor is it at all consistently related to the ratio of the internal concentrations of iron and manganese. There seems, however, no doubt that the content of manganese in the plant and the incidence of symptoms depend upon the ratio of the concentrations of iron and manganese in the external solution, antagonistic phenomena possibly being involved.

Boron deficiency or toxicity symptoms have likewise been said to depend upon the ratio of calcium to boron in the plant rather than on the actual boron content (see Table XIV) In tobacco the ratio would appear to be a better nutritional index than the boron content of the material, though in the data for oats and soybeans there seems to be no reason to prefer one to the other.

Table XIV

Relation of boron deficiency and toxicity symptoms to plant composition.

	Symptoms of boron deficiency	Normal	Symptoms of boron toxicity
Tobacco (*Drake et al.*, 1941)			
p.p.m. boron in plant dry matter	4—5	4—5	— —
Ratio calcium/boron in plant	1500—2100	1275—1340	——
Tobacco (*Jones and Scarseth*, 1944)*			
p.p.m. boron in plant dry matter	——	18—32	23—176
Ratio calcium/boron in plant	——	1302—1690	183—1009
Oats (*Jones and Scarseth*, 1944)			
p.p.m. boron in plant dry matter	——	15—50	44—400†
Ratio calcium/boron in plant	——	170—780	17—282
Soybeans (*Cook & Millar*, 1940; *Muhr*, 1941.)			
p.p.m. boron in plant dry matter	——	45—60†	75—100
Ratio calcium/boron in plant	——	53—359†	114—191

*Statement as to incidence of symptoms somewhat ambiguous.
†Including plants with slight toxicity symptoms.

There is no reason to suppose that ratios in general are likely to be of greater use in diagnostic work than the content of the elements individually. This is not to deny that diagnosis of the nutritional status in respect of one element on a basis of its concentration in the plant may not need modification according to the level found for another element ; Lundegårdh has shewn conclusively (1941) that this is sometimes the case. But the computation of ratios is not in general the best way of making allowance for such effects, and its adoption as a general practice may well obscure relationships which otherwise would be patent.

Among the nutrient ratios which have been used from time to time as diagnostic criteria may be mentioned that of nitrogen to phosphorus, which has been used as an index of both nitrogen and phosphorus deficiency in oat grain (Atterberg, 1888a, 1889 ; Stahl-Schröder, 1904), barley straw (Godlewski, 1901), potato tubers (Godlewski, 1901), wheat straw (Münter, 1919), beet tops and roots (Münter, 1920), apple leaves and wood (Thomas and Anthony, 1927), grape-vine wood (Vinet, 1932a, 1933, 1934, 1935, 1937, 1938), cacao leaves (McDonald, 1935 ; McDonald and Rodriguez, 1935), grapefruit leaves (Hardy and Rodriguez, 1935) ; and pine seedlings (Gast, 1937) ; that of potassium to nitrogen, used as an index of potassium nutrition by Münter (1919, 1920) in wheat straw and beet tops and roots, by Gast (1937) in pine seedlings and by the Trinidad investigators (Hardy, 1937 ; Hardy and Rodriguez, 1935 ; McDonald, 1933, 1935 ; McDonald and Rodriguez, 1935) for leaves of cacao and grapefruit, and as an index of nitrogen nutrition by Godlewski (1901) in potato tubers ; that of potassium to phosphorus, used as an index of potassium nutrition by Godlewski (1901) in barley straw and potato tubers, by Beauchamp *et al.* (1934,

1935) in sugar cane leaves and by McDonald and Rodriguez (1935) in cacao leaves, and for both potassium and phosphorus nutrition in vine leaves by Herschler (1933) ; that of potassium to calcium as an index of deficiency of the former in barley straw (Godlewski, 1901), grapefruit leaves (Hardy and Rodriguez, 1935 ; Hardy *et al.*, 1935) ; and other types of sample (Bower and Pierre, 1944) ; that of potassium to magnesium for potassium deficiency in barley straw (Godlewski, 1901) ; that of nitrogen to silicon in wheat straw for nitrogen deficiency (Münter, 1919) ; and that of copper to nitrogen in pear leaves for copper deficiency (Oserkowsky and Thomas, 1938) Sometimes more complex ratios have been suggested ; for instance, Beauchamp and his colleagues (Beauchamp *et al.*, 1934, 1935 ; Beauchamp and Lazo, 1938) considered the ratio of potassium to the sum of nitrogen and phosphorus (as pentoxide) a good index of potassium deficiency in sugar cane leaves, and he later (1942) suggested the ratio of potassium to the sum of calcium and magnesium oxides for the same purpose, similarly to Stanford *et al.* (1942) and Bower and Pierre (1944). Münter (1919) in wheat straw even used the proportion of potassium to the sum of nitrogen and the oxides of calcium and magnesium in this way. Menchikowsky and Puffeles (1935) suggested that the ratio of univalent to divalent cations in grapefruit leaves was of importance.

By far the most prolific writers who have concerned themselves with the ratios between the different nutrient elements in plant tissue have been those of the " foliar diagnosis " school. Their methods have already been briefly described (p. 41). The sum of the percentages of nitrogen, phosphorus (as P_2O_5) and potassium (as K_2O) in the plant material is found, and called the " quantity " or " intensity " of nutrition ; the percentages may then be recomputed as equivalents, and each of the three nutrients is expressed as a percentage of their sum, the three resulting figures forming the " NPK-unit ", " equilibrium " or " quality " index of nutrition. These latter values are generally plotted in trilinear co-ordinates (the distance of a point from the three sides of an equilateral triangle representing the proportion of each nutrient in the "NPK-unit "), and the displacement of any point from that representing the optimum (corresponding with a particularly good yield) indicates the particular type and extent of the nutritional "disequilibrium " from which the plant is suffering. Sometimes the " intensity " figure is adduced as reason for a modification in the deductions from the " NPK-unit ", but more often it is disregarded. Where calcium and magnesium are determined the values are used with those for potassium to form a " K-Ca-Mg unit " similar to the " NPK-unit " described above.

This " foliar diagnosis " work must be subject to much the same criticisms as other work involving the use of ratios ; unless it is demonstrated experimentally that the " NPK-unit " is related more closely to the growth and yield of the plant than the individual nutrient percentages from which it is derived the extra computational work it demands cannot be justified and it may even obscure nutritional relationships unnecessarily. Such a demonstration has never been made. It is true that, where the " intensity " is also quoted, no information is lost by expressing the results in the " NPK-unit " form, and if the " intensity " were used as a third dimension to the trilinear co-ordinates in which the " NPK-unit " is plotted (as suggested by Lagatu and Maume, 1934a) it might be possible to express all the relationships latent in the material. This, however, has never been done, and without an experimental demonstration it is difficult to believe that the method of expression used in " foliar diagnosis " is the best. The work of the " foliar diagnosis " school has had considerable influence, and among those workers who have sometimes expressed their results in the " foliar diagnosis " form are Beauchamp (1939, 1940, 1940a, 1942 ; Beauchamp and Alvarino, 1940), Clements *et al.* (1941) and Borden (1942, 1944). Craig (1938, 1939) also has expressed his results for nitrogen, potassium and phosphorus analyses of sugar cane leaves as percentages of their total, but using the percentage concentrations in the plant material instead of the equivalent concentrations. He claimed (1939) that the ratios computed in this way differed less between varieties grown under the same conditions than did the original percentage figures, and considered this an advantage.

In Table XV are listed values of the various ratios which have from time to time been proposed as " limiting " or " optimal " ; the optimal values quoted by the Pennsylvania workers are omitted because it is not claimed that they apply more widely than to the actual experiment and season under consideration.

Table XV.

Standard ratios of nutrient content proposed in the literature.

Plant	Ratio	Stage of development.	Organ	Standard value		Reference
BARLEY (*Hordeum vulgare*)						
	P_2O_5 : N	Harvest	Straw	P inadequate	<1:5	Godlewski, 1901
	K_2O : CaO	Harvest	Straw	K inadequate	<5:4	Godlewski, 1901
	K_2O : P_2O_5	Harvest	Straw	K inadequate	<5:2	Godlewski, 1901
	K_2O : MgO	Harvest	Straw	K inadequate	<5:1	Godlewski, 1901
COTTON (*Gossypium* spp)						
	Ca : (K+Na)	Aug.	Plant	Optimum	<1:1 (A)	Cooper & Garman, 1943
GRAPE (*Vitis vinifera* etc).						
	N : P_2O_5 : K_2O	Mean of several successive samples.	Basal leaves of fruiting shoots	Optimum	=41:8:51	Lagatu, 1940 ; Lagatu and Maume, 1936a, 1936e, 1938, 1938b, 1938c
	N : K_2O	June-July	Basal leaves of fruiting shoots	Optimum	=4:5	Lagatu, 1940
	K_2O : P_2O_5	Autumn	Leaves	Normal	=2:1	Herschler, 1933
LUCERNE (*Medicago sativa*)						
	Ca : K	———	Tops	Yield reduced	>4:1 (A)	Hunter *et al.*, 1943 ; Bear & Prince, 1945
OATS (*Avena sativa*)						
	N : P_2O_5	Beginning of flowering	Tops	Optimum	=100:45	Atterberg, 1889
	N : P_2O_5	Harvest	Grain	Optimum	=100:55	Atterberg, 1889
	N : P_2O_5	Harvest	Grain	Optimum nutrient balance in soil	=100:35-40	Stahl-Schröder, 1904
	N : K_2O	Harvest	Grain and straw respectively	Optimum	=1 : 1	Atterberg, 1889
POTATO (*Solanum tuberosum*)						
	N : P_2O_5 : K_2O	Harvest	Tubers	Normal	=10:8:3	Godlewski, 1901
	N : P_2O_5 : K_2O	Mean of several successive samples	Basal leaves of primary shoots	Optimum	=38:4:58	Lagatu & Maume, 1934c, 1935b
	N : P_2O_5	Harvest	Tubers	N inadequate	<2:1	Godlewski, 1901
	N : K_2O	Harvest	Tubers	N inadequate	<3:5	Godlewski, 1901
	K_2O : P_2O_5	Harvest	Tubers	K inadequate	<3:1	Godlewski, 1901
SCOTS PINE (*Pinus sylvestris*)						
	N : P : K	Seedling	Plant	Normal	=100:12:35	Gast, 1937 ; from data of Manshard, 1938
SOYBEAN (*Glycine soja*)						
	Ca : B	Harvest	Plant (?)	Optimum	=500 : 1	Jones & Scarseth, 1944, from data of Muhr, 1941
SUGAR BEET (*Beta vulgaris*)						
	N : P_2O_5	Harvest	Tops	N inadequate	<20:7	Münter, 1920
	P_2O_5 : N	Harvest	Tops	P inadequate	<1:5	Münter, 1920, 1920a
	P_2O_5 : N	Harvest	Roots	P inadequate	<1:4	Münter, 1920
	K_2O : N	Harvest	Leaves	K inadequate	<1:1	Münter, 1920a
	K_2O : N	Harvest	Roots	K inadequate	<17:20	Münter, 1920
	Ca : B	———	———	Optimum	=100:1	Jones & Scarseth, 1944, from data of Cook & Millar, 1940
SUGAR CANE (*Saccharum officinarum*)						
	N : P_2O_5 : K_2O	———	Third leaf blades from apex	Optimum	=50:12:38	Craig, 1938
	K_2O :(N+P_2O_5)	9 months	Leaves	Good growth	>2:1 (B)	Beauchamp *et al.*, 1934
	K_2O : P_2O_5	9 months	Leaves	Good growth	>3:1 (B)	Beauchamp *et al.*, 1934

Plant	Ratio	Stage of development.	Organ	Standard value		Reference
TOBACCO (*Nicotiana tabacum*)						
	N : K	———————	Cured leaves	Optimum	=8-11:10	Gribbins *et al.*, 1941
	K : Mg	———————	Leaves	Optimum quality	=59:10	Drake & Scarseth, 1940
	Ca : B	Flowering (?)	Plant (?)	Normal	<1340:1	Drake *et al.*, 1941
	Ca : B	Flowering (?)	Plant (?)	Optimum	=1200:1	Jones & Scarseth, 1944, from data of Drake *et al.*, 1941
WHEAT (*Triticum vulgare*)						
	N : P_2O_5	Harvest	Straw	N inadequate	<5 : 3	Münter, 1919
	N : SiO_2	Harvest	Straw	N inadequate	<3:50	Münter, 1919
	P_2O_5 : N	Harvest	Straw	P inadequate	<7:20	Münter, 1919
	K_2O : N	Harvest	Straw	K inadequate	<2:1	Münter, 1919
	K_2O : (N : CaO + MgO)	Harvest	Straw	K inadequate	<1:1	Münter, 1919

NOTES: A. Calculated as equivalents.
B. In alcohol extract.

Where optimal values for nutrient content or ratios of nutrients in the plant have been determined, it is possible, instead of attempting to forecast the yield increment to be expected from a given application to plants with a given nutrient content, to proceed by trial and error. That is, an arbitrary amount of fertilizer is applied, and if this fails to raise the nutrient content to the optimum a further application is made. This procedure has been recommended by the "foliar diagnosis" school (see p. 41) and by Yuen and Hance (1939) among others. It is, however, uneconomic, since in the region immediately below the optimum yield rises only slowly with the increasing nutrient supply and internal concentration; consequently this method of using plant analyses as a guide to fertilizer treatment can only be recommended where the cost of the latter forms no more than a very small proportion of the value of the crop.

INTERPRETATION BASED ON COMPARISON OF GOOD AND BAD PLANTS FROM THE SAME FIELD OR PLANTATION.—Many investigators have attempted to avoid the necessity of setting up standard values, curves or ratios for plant composition by confining their comparisons to those between "good" and "bad" plants growing in the same field or plantation (Joulie, 1876; Stahl-Schröder, 1904; Hester 1941, etc.). This procedure is subject to the objection that, without knowledge of the effect of treatments on the plants, it is impossible to be sure whether any differences in composition are causes, effects, or merely concomitants of the differences in growth or appearance of the plant (c.f. Lilleland and Brown, 1940; Guest, 1943). This is true even where it is possible to demonstrate (as suggested by Chapman, 1941) a correlation between plant growth and the content of a particular nutrient. This comparison of "good" and "bad" plants is virtually the only means of attacking by plant analysis the problem of the etiology of unidentified physiological disorders (see p. 20), but it can in no way be regarded as a substitute for the establishment of standards for nutrient content.

FACTORS AFFECTING THE USE OF PLANT ANALYSIS FOR DEFICIENCY DIAGNOSIS.

Weather Conditions.—There is abundant evidence that external factors other than nutrient supply affect the concentrations of the nutrient elements within the plant. Illumination, for instance, has been shewn to affect the phosphorus and potassium content of white pine seedlings (Mitchell, 1936) and the nitrate content of beet (R.I. agric. Exp. Sta., 1935) and cereals (Wark, 1938, 1939)—the latter to such an extent that only samples taken in bright weather were considered to give reliable diagnostic indications. Water supply or rainfall has often been shewn to affect nutrient content (Tollens, 1902; Pfeiffer *et al.*, 1912, 1913; Richards, 1932; Daniel and Harper, 1934; Beaumont and Snell, 1935; Emmert, 1936; Yates and Watson, 1939; Lilleland and Brown, 1941; Green, 1943) though it is often difficult to know to what extent this

effect may be due to greater amounts of nutrients being made available to the plant. The great variations in nutrient content of plants as a result of weather (see, for instance, Stahl-Schröder, 1904 ; Ames, 1910 ; Münter, 1919, 1920 ; Borden, 1936 ; Yates and Watson, 1939) are partly to be ascribed to direct effects of weather conditions on the plant, partly to their effect on the soil.

As already indicated (p. 60) the fact that environmental conditions cause alterations in the percentage nutrient content need in no way affect the course of analytical diagnosis, provided they do not also affect the relation between the increase in yield as a result of fertilizer treatment and plant composition. Though Pfeiffer *et al.* (1912) maintained that the percentage increase in yield with treatment corresponding to a given internal nutrient concentration was unaffected by external factors, there is some evidence that this is not strictly true (Stahl-Schröder, 1904 ; Ulrich, 1943 ; Thomas *et al.*, 1943a ; Boynton and Burrell, 1944 ; Hibon, 1944). Nevertheless Lundegårdh (1941) found his standard values applied tolerably well to different seasons ; as already shewn (p. 107) Münter's (1919, 1920) results from five consecutive and very different seasons give quite a good correlation between yield increase and nutrient percentage ; and the fact that Lagatu and Maume (see Table XV) have regarded their optimum composition for grape-vine leaves as applying to more than one season points in the same direction. Boynton and Compton (1945) report that seasonal differences in weather do not affect the relation between potassium and magnesium content of apple leaves and the incidence of deficiency symptoms, but that the optimum nitrogen content for fruit colour may differ with climate.

The most serious attempts to make allowance for such possible effects of weather differences have taken the form of trying to find some characteristic of the plant serving as an index of these differences, such as plant colour or sugar content (see p. 43) ; Emmert (1942), among others, has indicated the need for carbohydrate determinations. Clements and Kubota (1942) suggested determination of the water content of the sheaths surrounding the elongating part of the sugar cane as an index of moisture relations. Wark's (1938, 1939) avoidance of samples taken in dull weather has been mentioned ; likewise, Craig and Halais (1944) do not sample sugar cane leaves immediately after a drought or cyclone. Soulmagnon (1933) considered foliar diagnosis should be used only when water supplies were adequate. Yuen and Hance (1939) quote different critical values for the nitrogen content of sugar cane leaves under favourable and unfavourable weather conditions (see Table XII).

Pests and Diseases.—To the factors affecting the diagnostic use of plant analysis must probably be added pests and diseases. Though there is little experimental evidence on the subject, it would seem to be a sound principle to avoid sampling diseased plants (other than plants suffering from the nutritional disorder under investigation—see pp. 19-40, 69) for diagnostic purposes—even though nutrient deficiency may sometimes result in increased susceptibility to disease (Eaton, 1944). Likewise it is probably desirable to reject for purposes of determining standard values yield results derived from plants suffering to any marked extent from a pest or disease, and to make it clear that diagnostic conclusions only apply to otherwise normal and healthy plants.

Fixation of Nutrients by the Soil.—Differing fixation of nutrients by different soils is a factor which it is risky to neglect, and which can only be estimated—short of field or pot trials—by examination of the soil itself. Lundegårdh's (1934) original plan in his "Triple Analysis" method was to analyse the soil as well as the plant, which would have enabled him to allow for this factor ; later, however, he considered that the additional information given by soil analysis in respect of the three principal nutrients was insufficient to justify the additional labour. He found (1941) that his standard values applied equally well to soils of very different type.

Variety.—A factor to which little attention has been devoted in previous pages is the influence of variety in diagnostic work. There is abundant evidence that the differences in genetical constitution between varieties of cultivated plants may include differences affecting their mineral composition when grown under the same conditions—for instance in oats (Lundegårdh, 1931, 1932 ; Rademacher, 1937), apple (Wallace, 1931 ; Piper, 1936 ; Batjer and Magness, 1939), gooseberry (Wallace, 1931), tomato (Jones *et al.*, 1944), wheat (Tisdal, quoted by Lundegårdh, 1932 ; Maume and Dulac, 1934, 1935a, 1936, 1937, 1938, 1938a ; Maume and Bouat, 1937), sugar cane (Borden, 1936 ; Craig, 1938, 1939 ; Beauchamp and Alvarino 1940), grapefruit (Fudge, 1938, 1939), grape vine (Scott, 1941, 1944) and cotton (Crowther, 1936). Other workers have found only small or inconsistent differences in composition between varieties (Stahl-

Schröder, 1904; Poehlmann, 1935; Brandenburg, 1939; Yates and Watson, 1939; Lilleland and Brown, 1941, 1942; Carson *et al.*, 1941; MacVicar *et al.*, 1941; Batjer and Haller, 1942), but it seems clear that in many cases varietal differences are too large to be disregarded.

A variety used as a rootstock may not only differ in composition from other such varieties (Roach, 1930, 1931, 1933) but also affect that of the scion variety (Eaton and Blair, 1935; Vaidya, 1938; Lagatu and Maume, 1939; Goodall, 1945a; Haas, 1945a).

If varieties differ not only in composition but also in potential fertilizer response corresponding to a particular mineral content, diagnosis will be seriously inconvenienced by the necessity for setting up separate standard values for each variety. It seems, however, that in many cases the varietal differences in composition represent simply differing ability to absorb nutrients from the substrate in question, and not differing reaction to a given internal concentration. Where this is true, or where the different composition is ascribable to some other non-nutritional difference between the varieties, such as the formation of seedless fruit (Fudge, 1938, 1939), standard values may apply without modification according to variety. Craig (1941) came to the conclusion that " no very great error will be introduced if " the same optimal values for nutrient concentrations in sugar cane leaves " are used for any of the varieties so far studied," though later he and Halais (1944) quoted different optima for different varieties, basing them simply on their differing leaf composition when the varieties were grown side by side. In some cases, however, the relation of plant development to internal nutrient concentration does indeed appear to differ from variety to variety. Wallace (1940), for instance, found the limiting value for magnesium deficiency in the apple to be different in Laxton's Superb from that in other varieties, and Ravikovitch and Bidner (1937) came to similar conclusions in regard to chloride injury of the grape vine. Walsh and Cullinan (1945) found that the differing susceptibility of pea varieties to manganese deficiency was not accompanied by any corresponding differences in manganese content. Lineberry and Burkhart (1943) found that in strawberry the calcium content of plants of the variety Klondike showing symptoms of calcium deficiency fell well within the normal range for the variety Blakemore (see Table I). Crowther (1936) found that the cotton variety Gisa 7 had a particularly high nitrogen content, yet responded as well to nitrogenous fertilizers as the other varieties studied. Emmert (1942a) found the optimal nitrogen content (2% acetic acid extract) in tomato petioles to be higher in restricted-vine varieties than in those of a free-vining habit. Nevertheless, a number of investigators have expressed the opinion that relationships between fertilizer response and plant composition will hold with little modification over wide groups of plants; Lundegårdh (1941) considered that his results with oats would apply broadly to other cereals, Neller (1935) found similar optimal sap phosphorus concentrations in the various species with which he worked and Wallace (1941; Wallace and Osmond, 1941) stated that the limiting values for potassium and magnesium deficiency, which he had found in work mainly with the apple, could be extended very generally to other fruit plants. But the data in Tables, I, II, XII and XV bear eloquent witness to the fact that critical values cannot be expected to apply more widely than to a group of related plants unless some new and much more fundamental basis for expressing such values can be found.

Fruiting.—Differences in the bearing behaviour of fruit plants may be associated with considerable differences in the composition of the vegetative organs, on account of the heavy drain on the plant's nutrient reserves caused by fruit production. Such differences may even be apparent between different portions of the same plant (Lagatu and Maume, 1938c; Fudge, 1938, 1939). Thomas (1945), on the other hand, found little difference between the composition of leaves from fruiting and non-fruiting shoots of apple trees. Where the cropping behaviour of a plant varies considerably from year to year, it is clear that its nutrient requirements over a period of years could not be satisfactorily predicted from analysis of samples taken in one year only, unless account were taken of the fruit actually borne in that year (Hoagland and Arnon, 1941). Lilleland (1933) has pointed out that uncertainty as to the crop to be borne by plum trees will interfere with use of analyses of leaves sampled early in the season for predicting the probability of leaf scorch later.

THE PLACE OF PLANT ANALYSIS AMONG OTHER METHODS OF NUTRITIONAL DIAGNOSIS

COMPARISON OF PLANT ANALYSIS WITH FIELD TRIALS AS A DIAGNOSTIC METHOD.

It has been stated that the field trial represents the ultimate test to which any other proposed method of nutritional diagnosis must be submitted. But as a diagnostic method the field trial is subject to a number of disadvantages. First: in its traditional form, the results cannot be used during the year in which it is set up; this objection is met by some recent modifications (Evans, 1942; Wallace, 1943) in which observations are made at an early stage of development on some plant character, such as stem growth rate or leaf colour, which is correlated with final yield—but in such cases this correlation is the crucial, and sometimes doubtful, point. Second: its results are subject to substantial errors; in a properly designed trial these errors are random and at the cost of additional labour may be reduced to any extent desired. Third: it makes very heavy demands upon labour. Thus, while an extensive set of field trials is essential for standardising the results of other diagnostic techniques, it is very probable that when it is necessary to answer the question of what nutritional treatment is required by a crop about to be grown or already growing in a particular field, such other techniques may be more appropriate than an *ad hoc* field trial.

If plant analysis be considered against the background of these disadvantages of the field trial as a diagnostic method, it will readily be seen that in regard to labour costs, at least if the "capital expenditure" needed to set up standard values be disregarded, plant analysis is much to be preferred. Lindner (1944), for instance, reports that samples may be analysed for the five principal nutrient elements at the rate of two per hour, with a very satisfactory degree of chemical accuracy, and Wolf (1944a) quotes the figure of twenty-four samples analysed per day for three elements; even if time is added for the collection and preparation of the samples it will be seen that the labour required is incomparably less than for field trials. To some of the methods for rapid testing of plant material in the field this applies with even greater force. The errors of diagnosis by plant analysis will not always be random, and cannot always, like those of field trials, be diminished indefinitely by increased replication—for the standard values or curves on comparison with which the diagnosis is based are necessarily themselves subject to error; nevertheless an estimate by plant analysis based on standards derived from an extensive series of field trials may be nearer to the true yield response than an estimate derived from a field trial on the actual site (Lundegårdh, 1941; Thomas *et al.*, 1942). In respect of basal fertilizer dressings for annual crops, plant analysis may suffer from the same disadvantage as an *ad hoc* field trial—that results will only be available for subsequent crops, unless it is possible before planting time to obtain plant material (from weeds or from the previous crop) for which standard analytical values *in relation to the performance of the subsequent crop* are available. For top or side dressings to established plants, however, results of plant analysis may be put to immediate practical application, and it would be unnecessary, as with a field trial, to wait until the harvest had been completed before drawing conclusions. With perennial crops it may be necessary to carry a field trial on for several years before the full effect of the treatments can be seen, but plant analysis (given suitable standardization) can give an immediate forecast of the response to treatment. Some of the advantages of plant analysis in labour and time over *ad hoc* field trials would be lost if it were necessary to grow plants specially to provide the samples for analysis—as has been suggested for instance by Münter (1919, 1920, 1920a).

While plant analysis can often provide a sensitive index of the need for nutrients in relatively poor supply, it is rather insensitive to changes in the supply level of nutrients adequate in relation to other "limiting factors." Very generally speaking, the analysis of plants not receiving special treatments will often show only which nutrient is "limiting" (Wallace, 1928a;

Thornton, 1932; Emmert, 1934; McDonald, 1934; Thornton *et al.*, 1934; Scarseth, 1941, 1941a; Ulrich 1944) and not those to which responses would be obtained if the supply of the "limiting" nutrient had been itself increased; sometimes, however (Carolus *et al.*, 1938; Wallace, 1943; Roberts, 1945) deficiency of more than one nutrient may be shewn simultaneously.

It must be remembered that, while plant analysis may provide a good index of the nutritional status of the plant, the response of the plant to fertilizer treatments applied to the soil will also depend upon the nature of the soil. This is clearly recognized by the "Foliar Diagnosis" school (Lagatu and Maume, 1936e). Too much stress should not be laid upon this, for over a wide range of soils differences in nutrient fixation will not greatly affect the value of diagnosis by plant analysis—and will in any case only affect the extent of response, and not its existence or direction. Still, it seems probable that information about the soil would often prove a valuable means of correction to diagnoses derived from plant analysis.

COMPARISON OF PLANT ANALYSIS WITH SOIL ANALYSIS AS A DIAGNOSTIC METHOD.

Soil analysis for diagnostic purposes, like plant analysis, represents a great saving in labour in comparison with field trials, and has the advantage over both methods that results may be obtained with very little delay at any time of the year. It has also the important advantage over plant analysis that it is equally sensitive to nutrients in relatively good and relatively poor supply. In comparisons of forecasts of fertilizer response by plant analysis and by soil analysis, it should be remembered that attention has been given continuously and on a wide scale over several decades to the development of methods of soil analysis and to their standardization against field trials, whereas the same can hardly be said of plant analysis. Nevertheless many investigators have in practice found plant analysis of greater value; this was Loehwing's (1928) view in his study of over-liming injury, and that of Emmert (1931) in his work on soil reaction, while Gilbert and Smith (1929) came to the same conclusion in regard to nitrogen nutrition of vegetable crops. Lundegårdh's (1934) method of "triple analysis" originally included analyses of soil and subsoil samples as well as of plant material; however, he found that very little information was lost by omitting the soil and subsoil analyses and so later confined his attention to the plant material. Lilleland and Brown (1941) found that effects of differing drainage on potassium nutrition of peach leaves were not revealed in soil analysis, but were clear from leaf analysis. Boynton (1942) found leaf analysis preferable for the diagnosis of potassium deficiency in fruit trees. Carolus *et al.* (1938) have pointed out that localized fertilizer applications may make it difficult to secure a representative soil sample, though in no way interfering with the use of plant analysis. Mitchell (1939) and Lundegårdh (1941) have drawn attention to the fact that plant analysis makes full allowance for the extent to which plant roots penetrate different soil horizons, whereas this can hardly be done in a technique of soil analysis alone. Among others who have compared soil and plant analysis techniques for the major nutrients, and found the latter often to be more useful are Liebscher *et al.* (1898), Ames (1910), Hester (1931) Sayre (1941), Scarseth (1943) and McCollam (1943). Diagnostic soil analysis for the trace elements has as yet been little developed, and here plant analysis appears to have an important role to play.

It has been suggested that a useful method of combining the techniques of soil and plant analysis would be to use soil analysis as a means of determining what basal fertilizer dressing should be applied before the crop is planted, and to use the results of subsequent periodical plant analysis to determine whether that basal dressing has been taken up by the crop, whether it has been adequate, and whether additional top or side dressings are needed.

COMPARISON OF PLANT ANALYSIS WITH THE USE OF DEFICIENCY SYMPTOMS AS A DIAGNOSTIC METHOD.

The only important remaining method of deficiency diagnosis is by the visual recognition of symptoms. This is a very direct and rapid method, but the symptoms of a disorder are not always as definite and as characteristic as might be wished (see p. 10). Confirmation that an abnormality is symptomatic of deficiency of a specific element is very desirable, and for this purpose the method of injection developed by Roach (see p. 8) seems particularly appropriate. In certain cases proof of a definite deficiency has been established beyond doubt by this method,

but in this connection further work requires to be done to determine the factors affecting response and the physiological changes accompanying the re-establishment of normal appearance of the leaves.

Where symptoms can be readily and definitely recognized this is probably the ideal method of diagnosis; but there is always the likelihood that, if the deficiency could have been identified and remedied before symptoms appeared, the final yield might have been higher than if treatment had to wait upon the recognition of symptoms. Furthermore there is abundant evidence that nutrient deficiencies not severe enough to produce recognizable symptoms cause a reduction in growth and yield though the same does not appear to be equally true of toxicity effects (Scofield and Wilcox, 1931; Eaton, 1944). It is in such cases of less severe deficiency (Lagatu and Maume, 1935e; Cullinan and Batjer, 1943; Lindner, 1944), and to indicate deficiency at an earlier stage than symptoms can be expected to appear (MacGillivray *et al.*, 1930; Hardy, 1937; Olson, 1942a; Green, 1943; Scarseth, 1943; Large, 1944, 1945), that plant analysis is likely to be a valuable supplement to the observation of deficiency symptoms. The use of plant analysis in confirming uncertain diagnoses based on symptoms or the results of injection cannot be questioned apart from its use in the many cases where no characteristic symptoms appear at all.

It thus appears that when a satisfactory technique has been worked out according to the principles set out in preceding sections, and standard values have been firmly based upon an extensive series of field trials, plant analysis should be of great value in combination with soil analysis, particularly for perennial crops and to indicate the need of annual crops for fertilizer treatments subsequent to planting time. While in many cases neither plant nor soil analysis can compete in ease and rapidity with the identification of symptoms of nutritional disorders as a means of diagnosis, they provide the possibility of preventing the appearance of such symptoms. Besides this use of plant analysis in what may broadly be termed advisory work, it can be very useful too in interpreting the results of fertilizer trials and in finding the cause of physiological disorders of unknown origin (see p. 20). But in the more practically important field of advisory work the great importance of care in selecting a technique and in the determination of standard values cannot be too strongly emphasized.

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